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THE BRITISH JOURNAL OF ANIMAL BEHAVIOUR

Official Journal of the Association for the Study of Animal Behaviour

Edited by

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Introducing Douglas Spalding

By J. B. S. HALDANE

Department of Biometry, University College, London

The following article was printed in Macmillan's Magazine, Vol. 27, pp. 282-293, 1873. Many, but not all, of the facts there described, have since been rediscovered. However, writers on instinct and related topics, not only in continental Europe and North America, but in Britain, do not refer to Spalding's work. This is the more remarkable as it was not ignored in his own time.

Spalding was born in London about 1840 of working class parents. He worked as a stonemason in Aberdeen, educated himself, and attended Professor Bain's lectures on psychology. He qualified as a barrister in London, but apparently never practised. In 1872 he read the paper here reprinted to the British Association. Mill and others at once saw his importance, and Lord Amberley appointed him tutor to his sons, one of whom, Bertrand (Earl) Russell, is still alive. Lord and Lady Amberley co-operated with him in the experiments in which he first showed that hand-reared swallows kept in cages too small to permit of flying, flew "perfectly" on the first opportunity. I hope that this work, and his work on piglets blindfolded at birth, will later be reprinted. Lord Amberley left provision in his will that Spalding was to continue as tutor to his sons. As the result of a legal action which attracted considerable attention at the time, this provision was set aside by a court of law, and the children were educated in the tenets of the Church of England. We must, I fear, abandon the attractive idea that Bertrand Russell's behaviour shows evidence of imprinting by Spalding, since he tells me that Spalding only actually acted as tutor to his elder brother. This brother however, as readers of his autobiography can ascertain, was no discredit to his tutor.

In 1877 Spalding died of phthisis. Had he lived even to the age of fifty, there can be little doubt that he would be recognized as the principal founder of what is now called ethology. His researches on the subject, with reviews of books on the more philosophical aspects of evolution, were regularly published in the early volumes of "Nature," and G. H. Lewes, in his "Problems of Life and Mind" cited his unpublished observations on a gosling reared away from water, which refused to enter a pond when first taken to one at the age of some months. Romanes also repeatedly referred to him; and a discussion of his work is found in the chapter on instinct in William James' "Principles of Psychology," which indeed brought him to my notice. Spurway, in a forthcoming article in this Journal, quotes James' conclusions in detail.

While parts of Spalding's discussion refer to controversies current eighty years ago, other parts are completely up-to-date. Thus the technique of Crusoe's suggested experiment is quite analogous to that by which Waddington (1953 *Evolution*, 7, 118-126) has evoked a new morphological character in *Drosophila melanogaster*. To give a complete parallel to Waddington, Crusoe should also have bred from those parrots which, in each generation, could not be taught to say "How do you do, Sir," and shown that the fraction of unteachable birds in their progeny increased in successive generations. Spalding's technique is equally up-to-date. His method of temporarily deafening young birds is clearly much simpler than that of rearing them in soundproof rooms, and could be applied to a number of problems.

Naturally we should like more details of his experimental work. I, for example, should like to know with what breeds of poultry he worked. If so important an instinct as broodiness is present in some breeds and absent in others, there may well be differences in juvenile behaviour. I therefore introduce this article in the belief that others will be stimulated to continue his work.

I must thank Macmillan & Co. Ltd. for their permission to republish this article, and for their courtesy in allowing me access to their files.

J. B. S. HALDANE

INSTINCT

WITH ORIGINAL OBSERVATIONS ON YOUNG ANIMALS

The exquisite skill and accurate knowledge observable in the lives of the lower animals, which men generally have regarded as instinctive—born with them—have ever been subjects of wonder. In the hands of the natural theologian, whose armoury has been steadily impoverished in proportion as mystery has given way before science, instinct is still a powerful weapon. When the divine expatiates on the innate wisdom and the marvellous untaught dexterity of beasts, birds, and insects, he is in little danger of being checked by the men of science. His learned enemies are dumb, when in triumph he asks the old question:—

“Who taught the nations of the field and wood
To shun their poison and to choose their food?
Prescient, the tides or tempests to withstand,
Build on the wave, or arch beneath the sand?”

The very little that our psychologists have done for instinct may be told in a few words. The only theory of instinct, of the nature of an explanation, is that put forward by Mr. Herbert Spencer as part of his philosophy of evolution; but, as a theory, it is only beginning to be understood and appreciated among scientific men; while some eminent thinkers question the reality of the phenomena to be explained. Professor Bain, our other psychologist, and his able following of trained disciples, simply discredit the alleged facts of instinct. Unfortunately, however, instead of putting the matter to the test of observation and experiment, they have contented themselves with criticising the few accidental observations that have been recorded, and with arguing against the probability of instinctive knowledge. In defending the Berkeleyan Theory of Vision, Professor Bain, in answer to the assertion that the young of the lower animals manifest an instinctive perception of distance by the eye, contends that “there does not exist a body of careful and adequate observations on the early movements of animals.” Writing long ago on the same subject, Mr. Mill also, while admitting that “the facts relating to the young of the lower animals have been long felt to be a real stumbling block in the way of the theory,” maintains that “our knowledge of the mental operations of animals is too imperfect to enable us to affirm positively that they have this instinct.” Denying

the facts, however, was not Mr. Mill’s mode of saving the theory. He was rather of opinion that the “animals have to us an inexplicable facility both of finding and selecting the objects which their wants require.” How very inexplicable, he conceives, their mental operations may possibly be, may be gathered from the fact of his suggesting an experiment to ascertain whether a blind duckling might not find the water as readily as one having sight. The position of psychologists of the too purely analytical school, however, is not that the facts of instinct are inexplicable; but that they are incredible. This view is set out most explicitly in the article on Instinct in “Chambers’s Encyclopaedia.” Thus: “It is likewise said that the chick recognizes grains of corn at first sight, and can so direct its movements as to pick them up at once; being thus able to know the meaning of what it sees, to measure the distance of objects instinctively, and to graduate its movements to that knowledge—all which is, in the present state of our acquaintance with the laws of mind, wholly incredible.” And it is held, that all the supposed examples of instinct may be—for anything that has yet been observed to the contrary—nothing more than cases of rapid learning, imitation, or instruction.

Thus it would appear that with regard to instinct we have yet to ascertain the facts. With a view to this end, I have made many observations and experiments, mostly on chicken. The question of instinct, as opposed to acquisition, has been discussed chiefly in connection with the perceptions of distance and direction by the eye and the ear. Against the instinctive character of these perceptions it is argued, that as distance means movement, locomotion, the very essence of the idea is such as cannot be taken in by the eye or ear; that what the varying sensations and feelings of sight and hearing correspond to, must be got at by moving over the ground—by experience. On the other hand, it is alleged that, though as regards man the prolonged helplessness of infancy stands in the way of the observer, we have only to look at the young of the lower animals to see that as a matter of fact they do not require to go through the process of learning

the meaning of their sensations in relation to external things; that chickens, for example, run about, pick up crumbs, and follow the call of their mother *immediately* on leaving the shell. For putting this matter to the test of experiment, chickens, therefore, are most suitable and convenient subjects. I have observed and experimented on more than fifty chickens, taking them from under the hen while yet in the eggs. But of these, not one on emerging from the shell was in a condition to manifest an acquaintance with the qualities of the outer world. On leaving the shell they are wet and helpless; they struggle with their legs, wings, and necks, but are unable to stand or hold up their heads. Soon, however, they may be distinctly seen and felt pressing against and endeavouring to keep in contact with any warm object. They advance very rapidly. I have seen them hold up their heads well, peck at objects, and attempt to dress their wings when only between four and five hours old. But there is no difficulty in conceiving that, with great spontaneity and a strong power of association, much might be learned in four or five hours. Professor Bain is of opinion, from observations of his own on a newly dropped lamb, that "a power that the creature did not at all possess naturally, got itself matured as an acquisition in a few hours." Accordingly, in the absence of precautions, the time that must elapse before chickens have acquired enough control over their muscles to enable them to give evidence as to their instinctive power of interpreting what they see and hear, would suffice to let in the contention that the eye and the ear may have had opportunities of being educated. To obviate this objection with respect to the eye, I had recourse to the following expedient. Taking eggs just when the little prisoners had begun to break their way out, I removed a piece of the shell, and before they had opened their eyes drew over their heads little hoods, which, being furnished with an elastic thread at the lower end, fitted close round their necks. The material of these hoods was in some cases such as to keep the wearers in total darkness; in other instances it was semi-transparent. Some of them were close at the upper end, others had a small aperture bound with an elastic thread, which held tight round the base of the bill. In this state of blindness—the blindness was very manifest—I allowed them to remain from one to three days. The conditions under which

these little victims of human curiosity were first permitted to see the light were then carefully prepared. Frequently the interesting little subject was unhooded on the centre of a table covered with a large sheet of white paper, on which a few small insects, dead and alive, had been placed. From that instant every movement, with the date thereof, as shown by the watch, was put on record. Never in the columns of a Court Journal were the doings of the most royal personage noted with such faithful accuracy. This experiment was performed on twenty separate chickens at different times, with the following results. Almost invariably they seemed a little stunned by the light, remained motionless for several minutes, and continued for some time less active than before they were unhooded. Their behaviour, however, was in every case conclusive against the theory that the perceptions of distance and direction by the eye are the result of experience, of associations formed in the history of each individual life. Often at the end of two minutes they followed with their eyes the movements of crawling insects, turning their heads with all the precision of an old fowl. In from two to fifteen minutes they pecked at some speck or insect, showing not merely an instinctive perception of distance, but an original ability to judge, to measure distance, with something like infallible accuracy. They did not attempt to seize things beyond their reach, as babies are said to grasp at the moon; and they may be said to have invariably hit the objects at which they struck—they never missed by more than a hair's breadth, and that too, when the specks at which they aimed were no bigger, and less visible, than the smallest dot of an *i*. To seize between the points of the mandibles at the very instant of striking seemed a more difficult operation. I have seen a chicken seize and swallow an insect at the first attempt; most frequently, however, they struck five or six times, lifting once or twice before they succeeded in swallowing their first food. The unacquired power of following by sight was very plainly exemplified in the case of a chicken that, after being unhooded, sat complaining and motionless for six minutes, when I placed my hand on it for a few seconds. On removing my hand the chicken immediately followed it by sight backward and forward and all round the table. To take, by way of example, the observations in a single case a little in detail:—

A chicken that had been made the subject of experiments on hearing, was unhooded when nearly three days old. For six minutes it sat chirping and looking about it; at the end of that time it followed with its head and eyes the movements of a fly twelve inches distant; at ten minutes it made a peck at its own toes and the next instant it made a vigorous dart at the fly, which had come within reach of its neck, and seized and swallowed it at the first stroke; for seven minutes more it sat calling and looking about it, when a hive-bee coming sufficiently near was seized at a dart and thrown some distance, much disabled. For twenty minutes it sat on the spot where its eyes had been unveiled without attempting to walk a step. It was then placed on rough ground within sight and call of a hen with a brood of its own age. After standing chirping for about a minute, it started off towards the hen, displaying as keen a perception of the qualities of the outer world as it was ever likely to possess in after life. It never required to knock its head against a stone to discover that there was "no road that way." It leaped over the smaller obstacles that lay in its path and ran round the larger, reaching the mother in as nearly straight line as the nature of the ground would permit. This, let it be remembered, was the first time it had ever walked by sight!'

It would be out of place here to attempt to indicate the full psychological bearing of these facts. But this much may be affirmed, that they put out of court all those who are prepared only to argue against the instinctive perception by the eye of the primary qualities of the external world. When stripped of all superfluous learning, the argument against this and every other alleged case of instinctive knowledge is simply that it is unscientific to assume an instinct when it is possible that the knowledge in question may have been *acquired* in the ordinary way. But the experiments that have been recounted are evidence that prior to experience chickens behave as if they already possessed an acquaintance with the established order of nature. A hungry chick that never tasted food is able, on seeing a fly or a spider for the first time, to bring into action muscles that were never so exercised before, and to perform a series of delicately adjusted movements that end in the capture of the insect. This I assert as the result of careful observation and experiment; and it cannot be answered but

by observation and experiment at least as extensive. It is no doubt common for scientific men to discredit new facts, for no other reason than that they do not fit with theories that have been raised on too narrow foundations; but when they do this they are only geologists, or psychologists—they are not philosophers.

Before passing to the perceptions of the ear, it may be mentioned that, instead of hooding chickens, which had the advantage of enabling me to make many interesting observations on them when in a state of blindness, I occasionally put a few eggs, when just chipped, into a flannel bag made for the purpose. In this bag the hatching was completed artificially, and the chickens allowed to remain in the dark from one to three days. When placed in the light they deported themselves as regards sight in the manner already described. For the purpose of merely testing the perceptions of the eye or the ear this is by far the easier experiment. The hooding process requires considerable delicacy of manipulation, and the chickens are very liable to be injured.

¹ Since writing this article, I see it stated in Mr. Darwin's new book, "The Expressions of the Emotions in Man and Animals," that "the wonderful power which a chicken possesses only a few hours after being hatched, of picking up small particles of food, seems to be started into action through the sense of hearing; for, with chickens hatched by artificial heat, a good observer found that 'making a noise with a finger-nail against a board, in imitation of the hen-mother, first taught them to peck at their meat.'" My own observations give no countenance whatever to this view:—(1) I have frequently observed chickens finally hatched in a flannel nest over a jar of hot water and left undisturbed for a few hours, begin, immediately after the covering was removed, and while they still sat nestling together, to pick at each other's beaks and at specks of oatmeal when these were dropped on them, all noise being as far as possible avoided. (2) Each of the twenty chickens made subjects of the experiment described in the text, began to eat without any assistance from the sense of hearing; the greatest possible stillness being maintained and required during the experiment. (3) Chickens picked up food though rendered deaf while yet in the shell. One of these, deprived of both sight and hearing at its birth, was unhooded when three days old, and nine minutes after it vigorously pursued a large blue fly a distance of two feet, pecking at it several times: this bird proved perfectly deaf. Another with its ears similarly closed, was taken from the dark when a day and a half old, and when an experiment was being tried to ascertain whether it was perfectly deaf—which it turned out to be—it began to pick up and swallow small crumbs. What in this case really surprised me was that, the gum employed in closing its ears having also sealed up one of its eyes, it nevertheless picked up crumbs by sight of its one eye almost if not altogether as well as if it had had two.

With respect now to the space perceptions of the ear, which, in man at least, even Mr. Spencer regards as acquired by each individual. Chickens hatched and kept in the said bag for a day or two, when taken out and placed nine or ten feet from a box in which a hen with chicks were concealed, after standing for a minute or two, uniformly set off straight for the box in answer to the call of the hen, which they had never seen and never before heard. This they did, struggling through grass and over rough ground, when not yet able to stand steadily on their legs. Nine chickens were thus experimented upon, and each individual gave the same positive results, running to the box scores of times, and from every possible position. To vary the experiment I tried the effect of the mother's voice on hooded chickens. These, when left to themselves, seldom made a forward step, their movements were round and round, and backward; but when placed within five or six feet of the mother, they, in answer to her call, became much more lively, began to make little forward journeys, and soon followed her by sound alone, though, of course, blindly keeping their heads close to the ground and knocking against everything that lay in their path. Only three chickens were made subjects of this experiment. Another experiment consisted in rendering chickens deaf for a time by sealing their ears with several folds of gum paper before they had escaped from the shell. I tried at different times to stop the ears of a good many in this way, but a number of them got the papers off, others were found not quite deaf, and only three remained perfectly indifferent to the voice of the mother when separated from them by only an inch board. These had their ears opened when between two and three days old, and on being placed within call of the mother hidden in a box, they, after turning round a few times, ran straight to the spot whence came what must have been very nearly, if not actually, the first sound they had ever heard. It seems scarcely necessary to make any comment on these facts. They are conclusive against the theory that, in the history of each life, sounds are at first but meaningless sensations; that the direction of the sounding object, together with all other facts concerning it, must be learned entirely from experience.

If now it be taken as established that in the perceptions of the eye and the ear, chickens at least manifest an instinctive knowledge of

the relations and qualities of external things, the popular belief that the special knowledge, the peculiar art and skill, so marked in the various species of animals, come to them mostly without the labour of acquisition, is at once freed from all antecedent improbability. In the way of direct evidence, the little that I have been able to observe in this wide field goes to prove that the current notions are in accordance with fact. We have seen that chickens follow the call of their mother before they have had any opportunity of associating that sound with pleasurable feelings; and one or two observations, which must be taken for what they are worth, support the general opinion that they have an equally instinctive dread of their more deadly enemies. When twelve days old one of my little *protégés*, while running about beside me, gave the peculiar chirr whereby they announce the approach of danger. I looked up, and behold a sparrow-hawk was hovering at a great height over head. Having subsequently procured a young hawk, able to take only short flights, I made it fly over a hen with her first brood, then about a week old. In the twinkling of an eye most of the chickens were hid among grass and bushes. The hen pursued, and scarcely had the hawk touched the ground, about twelve yards from where she had been sitting, when she fell upon it with such fury that it was with difficulty that I was able to rescue it from immediate death. Equally striking was the effect of the hawk's voice when heard for the first time. A young turkey, which I had adopted when chirping within the uncracked shell, was on the morning of the tenth day of its life eating a comfortable breakfast from my hand, when the young hawk, in a cupboard just beside us, gave a shrill chip, chip, chip. Like an arrow the poor turkey shot to the other side of the room, and stood there motionless and dumb with fear, until the hawk gave a second cry, when it darted out at the open door right to the extreme end of the passage and there, silent and crouched in a corner, remained for ten minutes. Several times during the course of that day it again heard these alarming sounds, and in every instance with similar manifestations of fear. Unfortunately, my hawk coming to an untimely end, I was prevented from proceeding with observations of this class. But these few were so marked and unmistakeable in their character that I have thought them worth recording.

There are instincts, however, yet to be mentioned, concerning the reality of which I have thoroughly satisfied myself. The early attention that chickens give to their toilet is a very useful instinct, about which there can be no question. Scores of times I have seen them attempt to dress their wings when only a few hours old—indeed as soon as they could hold up their heads, and even when denied the use of their eyes. The art of scraping in search of food, which, if anything, might be acquired by imitation—for a hen with chickens spends the half of her time in scratching for them—is nevertheless another indisputable case of instinct. Without any opportunities of imitation, when kept quite isolated from their kind, chickens began to scrape when from two to six days old. Generally, the condition of the ground was suggestive; but I have several times seen the first attempt, which consists of a sort of nervous dance, made on a smooth table. As an example of unacquired dexterity, I may mention that on placing four ducklings a day old in the open air for the first time, one of them almost immediately snapped at and caught a fly on the wing. More interesting, however, is the deliberate art of catching flies practised by the turkey. When not a day and a half old I observed the young turkey already spoken of slowly pointing its beak at flies and other small insects without actually pecking at them. In doing this, its head could be seen to shake like a hand that is attempted to be held steady by a visible effort. This I observed and recorded when I did not understand its meaning. For it was not until after, that I found it to be the invariable habit of the turkey, when it sees a fly settled on any object, to steal on the unwary insect with slow and measured step until sufficiently near, when it advances its head very slowly and steadily till within an inch or so of its prey, which is then seized by a sudden dart. If all this can be proved to be instinct, few, I think, will care to maintain that *anything* that can be learned from experience *may* not also appear as an intuition. The evidence I have in this case, though not so abundant as could be wished, may yet, perhaps, be held sufficient. I have mentioned that this masterpiece of turkey cleverness when first observed, was in the incipient stage, and, like the nervous dance that precedes the actual scraping, ended in nothing. I noted it simply as an odd performance that I did not understand.

The turkey, however, which was never out of my sight except when in its flannel bag, persisted in its whimsical pointing at flies, until before many days I was delighted to discover that there was more in it than my philosophy had dreamt of. I went at once to the flock of its own age. They were following a common hen, which had brought them out; and as there were no other turkeys about the place, they could not possibly learn by imitation. As the result, however, of their more abundant opportunities, I found them already in the full and perfect exercise of an art—a cunning and skilful adjusting of means to an end—bearing conspicuously the stamp of experience. But the circumstances under which these observations were made left me no room for the opinion that the experience, so visible in their admirable method of catching flies, was original, was the experience, the acquisition of those individual birds. To read what another has observed is not, however, so convincing as to see for oneself, and to establish a case so decisive more observation may reasonably be desired; at the same time, it can scarcely be attempted to set aside the evidence adduced, on the ground of improbability, for the *fact* of instinct: all that is involved in this more striking example, has, we venture to think, been sufficiently attested.

A few manifestations of instinct still remain to be briefly spoken of. Chickens as soon as they are able to walk will follow any moving object. And, when guided by sight alone, they seem to have no more disposition to follow a hen than to follow a duck, or a human being. Unreflecting on-lookers, when they saw chickens a day old running after me, and older ones following me miles and answering to my whistle, imagined that I must have some occult power over the creatures, whereas I simply allowed them to follow me from the first. There is the instinct to follow; and, as we have seen, their ear prior to experience attaches them to the right object. The advantage of this arrangement is obvious. But instincts are not conferred on any principle of supplying animals with arts very essential to them, and which they could not very well learn for themselves. If there is anything that experience would be sure to teach chickens, it would be to take care when they had got a piece of food not to let their fellows take it from them, and from the very first they may be seen to run off with a worm, pursued

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by all their companions. But this has been so stamped in their nature that, when they have never seen one of their kind, nor ever been disturbed in the enjoyment of a morsel, they nevertheless, when they get something larger than can be swallowed at once, turn round and run off with it.

Another suggestive class of phenomena that fell under my notice may be described as imperfect instincts. When a week old my turkey came on a bee right in its path—the first, I believe, it had ever seen. It gave the danger chirr, stood for a few seconds with outstretched neck and marked expression of fear, then turned off in another direction. On this hint I made a vast number of experiments with chickens and bees. In the great majority of instances the chickens gave evidence of instinctive fear of these sting-bearing insects; but the results were not uniform, and perhaps the most accurate general statement I can give is, that they were uncertain, shy, and suspicious. Of course to be stung once was enough to confirm their misgivings for ever. Pretty much in the same way did they avoid ants, especially when swarming in great numbers.

Probably enough has been said to leave no doubt in minds free from any bias on the subject, that in the more important concerns of their lives the animals are in great part guided by knowledge that they individually have not gathered from experience. But equally certain is it that they do learn a great deal, and exactly in the way that we are generally supposed to acquire all our knowledge. For example, every chicken, as far as my observations go, has to learn not to eat its own excrement. They made this mistake invariably; but they did not repeat it oftener than once or twice. Many times they arrested themselves when in the very act, and went off shaking their heads in disgust, though they had not actually touched the obnoxious matter. It also appeared that, though thirsty, they did not recognize water by sight, except perhaps in the form of dew-drops on the grass; and they had to some extent to learn to drink. Their first attempts were awkward; instead of dipping in their beaks, they pecked at the water, or rather at specks in the water, or at the edge of the water. All animals have a capacity to learn: each individual must learn the topography of its locality, and numerous other facts. Many dogs, horses, and elephants may be able to learn more than some men.

But I have no doubt that observation will bear out the popular belief that what may be called the professional knowledge of the various species—those special manifestations of practical skill, dexterity, and cunning that mark them off from each other, no less clearly than do the physical differences whereon naturalists base their classifications—is instinctive, and not acquired. As we shall see, the creatures have not in a vast multitude of instances the opportunity to acquire these arts. And if they had the opportunity, they have not individually the capacity to do so, even by way of imitation. We have seen as a matter of fact that it is by instinct that the chicken, and, I may now add, the turkey, scratch the surface of the earth in search of insects; also, that the turkey has a method of catching flies so remarkably clever that it cannot be witnessed without astonishment. Now chickens like flies no less than turkeys, and, though with less success, often try to catch them. But it is a significant fact that they do not copy the superior art. To give every opportunity of imitation, I placed a newly-hatched chicken with my turkey, when the latter was eleven days old. The two followed me about for several weeks, and when I deserted them they remained close companions throughout the summer, neither of them ever associating with the other poultry. But the chicken never caught the knowing trick of its companion—seemed, indeed, wholly blind to the useful art that was for months practised before its eyes.

Before passing to the theory of instinct, it may be worthy of remark that, unlooked for, I met with in the course of my experiments some very suggestive, but not yet sufficiently observed, phenomena; which, however, have led me to the opinion that not only do the animals learn, but they can also forget—and very soon—that which they never practised. Further, it would seem that any early interference with the established course of their lives may completely derange their mental constitution, and give rise to an order of manifestations, perhaps totally and unaccountably different from what would have appeared under normal conditions. Hence I am inclined to think that students of animal psychology should endeavour to observe the unfolding of the powers of their subjects in as nearly as possible the ordinary circumstances of their lives. And perhaps it may be because they have not all been sufficiently on their

guard in this matter, that some experiments have seemed to tell against the reality of instinct. Without attempting to prove the above propositions, one or two facts may be mentioned. Untaught, the new-born babe can suck—a reflex action; and Mr. Herbert Spencer describes all instinct as "compound reflex action;" but it seems to be well known that if spoon-fed, and not put to the breast, it soon loses the power of drawing milk. Similarly, a chicken that has not heard the call of the mother until eight or ten days old then hears it as if it heard it not. I regret to find that on this point my notes are not so full as I could wish, or as they might have been. There is, however, an account of one chicken that could not be returned to the mother when ten days old. The hen followed it, and tried to entice it in every way; still it continually left her and ran to the house or to any person of whom it caught sight. This it persisted in doing, though beaten back with a small branch dozens of times, and indeed cruelly maltreated. It was also placed under the mother at night, but it again left her in the morning. Something more curious, and of a different kind, came to light in the case of three chickens that I kept hooded until nearly four days old—a longer time than any I have yet spoken of. Each of these on being unhooded evinced the greatest terror of me, dashing off in the opposite direction whenever I sought to approach it. The table on which they were unhooded stood before a window, and each in its turn beat against the glass like a wild bird. One of them darted behind some books, and squeezing itself into a corner, remained cowering for a length of time. We might guess at the meaning of this strange and exceptional wildness; but the odd fact is enough for my present purpose. Whatever might have been the meaning of this marked change in their mental constitution—had they been unhooded on the previous day they would have run to me instead of from me—it could not have been the effect of experience; it must have resulted wholly from changes in their own organization.

The only theory in explanation of the phenomena of instinct that has an air of science about it, is Mr. Spencer's doctrine of Inherited Acquisition. The laws of association explain our intellectual operations, and enable us to understand how all our knowledge may be derived from experience. A chicken comes on a bee, and, imagining it has found a dainty

morsel, seizes the insect, but is stung, and suffers badly. Henceforth bees are avoided; they can be neither seen nor heard without a shudder of fear. Now, if we can realize how such an association as this—how that one individual learns by experience may, in any degree, be transmitted to the progeny of that individual—we have a key to the mystery of instinct. Instinct in the present generation is the product of the accumulated experiences of past generations. The plausibility of this hypothesis, however, is not appreciated by the majority of even the educated portion of the community. But the reason is not far to seek. Educated men, even materialists—their own positive statements to the contrary notwithstanding—have not yet quite escaped from the habit of regarding mind as independent of bodily organization. Hence it is, that while familiar with the idea of physical peculiarities passing by inheritance from one generation to another, they find it difficult to conceive how anything so impalpable as fear at the sight of a bee should be transmitted in the same way. Obviously, this difficulty is not consistent with a thorough belief in the intimate and invariable dependence of all kinds of mental facts on nervous organization. Let us, if possible, make this clear. The facts of mind that make up the stream of an individual life differ from material things in this important respect, that whereas the latter can be stored up, volitions, thoughts, and feelings, as such, cannot. Facts of consciousness cannot be thought of as packed away like books in a library. They have to be for ever produced, created, one after another; and when gone they are out of existence. Whatever associations may be formed among these, must depend for their permanence on the corresponding impress given to the nervous organism; and why should not this, which is purely physical, be subject to the law of heredity? Look at a friend as he lies in unconscious sleep. His sovereigns are in his pocket but where is his stock of ideas? Where is all he has learned from experience? You have simply a living machine; but such a machine that it can wake and exhibit all the phenomena of what we call a well-informed and cultivated mind. Suppose, now, that while you stand by, another organism, the same in every particle and fibre, is by some mysterious process formed direct from its elements. Outwardly you cannot tell the one from the other; but wake them and how will it be? Even then,

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will not the one being recognize you, and be as completely and indistinguishably your friend as the other? Will not the newly created man, by virtue of his identical material organization, possess the mind and character, the knowledge and feelings, the past, in a word, the personal identity of the other? I have made this extreme supposition in order that no doubt may be entertained as to the shape in which I hold the doctrine that for every fact of mind there is a corresponding fact of matter, and that, given the material fact, whether produced by repeated experiences in the life history of the individual, or inherited from parents, the corresponding mental fact will be the same. If this view be admitted, there can be no difficulty in conceiving how entrance into life on the part of the animals may be a waking up in a world with which they are, in greater or less degree, already acquainted. Instinct, looked at from its physical side, may be conceived to be, like memory, a turning on of the "nerve currents" on already established tracks: for no reason, we presume, can be suggested why those modifications of brain matter that, enduring from hour to hour and from day to day, render acquisition possible, should not, like any other physical peculiarity, be transmitted from parent to offspring. That they are so transmitted is all but proved by the facts of instinct, while these in their turn receive their only rational explanation in this theory of inherited acquisition. But the difficulty of the undisciplined mind lies, as we have said, in an inability to grasp the full significance of the doctrine that, in an individual life, it is the physical part alone that endures from day to day; that, strictly speaking, we cannot feel the same feeling or think the same thought twice over; that only as by pulling the bell-cord to-day we can, in the language of ordinary discourse, produce the sound we heard yesterday, can we, while the established connections among the nerves and nerve-centres hold, live our experiences over again.

This doctrine of inherited acquisition then, is, to say the least, a good working hypothesis in explanation of all those facts of instinct that may be conceived as built up, compounded out of, the accumulated experiences of innumerable generations. So far good. But it will occur to every reader that the peculiar depths of animal psychology are not yet explored. Two classes of phenomena still lie in the dark. First, there

are the many extraordinary and exceptional feats of dogs and other animals, which seem to be constantly falling under the observation of everybody except the few that are interested in these matters. Second, all the more wonderful instincts, especially those of insects, are such that it is hard, if at all possible, to conceive how they ever could have been derived from experience.

With regard to the first, it is not desirable to say much. Though volumes of marvellous stories have been written, I am not aware that any careful experiments have been tried, and, as the performances in question are of an exceptional character, it is perhaps but scientific caution not as yet to put too much stress on them. For my own part, though I have been very intimate with dogs, I have been singularly unfortunate in having never witnessed any of their more incomprehensible clairvoyant-like achievements. I have known them to do many surprising things, but I have always found that they had, or might have had, something to go upon—enough, coupled with quick intelligence, to account for their exploits. What may be said in this connection, if, indeed, it be prudent to say anything, is that, while we certainly cannot have all the data of experience from without of all the vastly different living things which people the earth, the air, and the ocean—while we certainly can have no trace of many feelings that arise from changes in the organisms of the different creatures, and which, instinctively interpreted, start them on lines of action—a host of statements, generally accepted as fact, suggest the opinion that even such animals as dogs, are alive to, conscious, sensible of influences that scarcely affect us, or wholly escape our cognition. If this be so, they have a basis of experience from which to start in their calculations that we want, and, if so, well may their actions seem to us, as Mr. Mill said, hopelessly inexplicable. Take, not the most remarkable, but the best-authenticated example of this class—the frequently alleged fact of dogs and other animals returning in a straight line, or by the most direct routes, through districts they had never before traversed, to places from which they had been taken by devious tracks, and even shut up in close boxes. To most people this is a phenomenon sufficiently incomprehensible. They are certain they themselves could do nothing at all like it. But there is in some men what may be just a hint of this

faculty. Most people that have lived only in cities are very soon lost in a strange and trackless district, and still sooner in a pathless wood; in the one case, after wandering this way and that for a few hours, in the other, after merely turning round a few times, they can tell nothing of the direction whence they came. But all men are not so easily lost; some, without consciously making notes, retain, after long wandering in such situations, a strong and often accurate impression, not of the ground they have gone over, but of the direction in which lies the place whence they started. Without attempting to throw any light on the mental chemistry of this perception, we would submit that in it may perhaps be found a clue to the mystery of those astonishing home-journeys of dogs, sheep, cats, pigeons, bees, &c., of which hundreds are on record.

It is, however, with the other dark enigma that we are more especially concerned. We do not think it necessary to examine the proof of the actuality of such marvellous instincts as those of bees and wasps. But for the too fond love of a theory we venture to think none would doubt the reality, or the instinctive character, of their "far-sighted," or, more correctly, blind provisions for the future. The problem before us is not whether for example, the male of the fish *Arius* does, and by instinct, hatch the eggs of the female in his mouth, but how such a singular mode of incubation ever has a beginning? Perhaps the most widely known instance of this class of instincts is the provision of the solitary wasp for the worm that will issue from her egg after her own death. She brings grubs—food that as a wasp she never tasted—and deposits them over the egg, ready for the larva she will never see. The life history of every insect exhibits instincts of this perplexing description. Witness the caterpillar, how at the proper time it selects a suitable situation and spins for itself a silken cocoon. It may be admitted at once that the creatures, as we behold them, never could have lived to acquire such instincts by any process of experience and inheritance of which we can conceive. Nor let it be supposed that it is only in the insect world, where all is so strange, that instincts are to be met with so essential to lives of the individuals or their progeny that without them the creatures in their present shape could never have existed. Of this kind are the first movements observable in the life of a bird, and which

take place within the shell. I have often observed the self-delivery of the chicken. The prison wall is not burst in pieces by spontaneous, random struggles. By a regular series of strokes the shell is cut in two—chipped right round in a perfect circle, some distance from the great end. Moreover, the bird has a special instrument for this work, a hard, sharp horn on the top of the upper mandible, which being required for no other purpose disappears in a few days. Obviously each individual bird, no more acquires the art of breaking its way out than it burnishes itself with the little pick hammer used in the operation; and it is equally clear that a bird could have never escaped from the egg without this instinct. Again, how were eggs hatched before birds had acquired the instinct to sit upon them? Or who will throw light on the process of such an acquisition? Nor are the subsequent phenomena easier of explanation. A fowl that never before willingly shared a crumb with a companion, will now starve herself to feed her chickens, which she calls by a language she never before used—may have never even heard—but which they are born to understand. Once more, it is clearly because she cannot do otherwise that a she-rabbit, when with her first young, digs a hole in the earth away from her ordinary habitation, and there builds a nest of soft grass, lined with fur stripped from her own body. But how as to the origin of this habit?

We need not accumulate examples of seemingly unfathomable instincts. And it may be confessed at once, that in the present state of our knowledge it would be hopeless to attempt to guess at the kinds of experiences that may have originally, when the creatures wore different shapes and lived different lives, wrought changes in their nervous systems that, enduring and being modified through many changes of form, have given to the living races the physical organisations of which these wonderful instincts are the corresponding mental facts. Nor, perhaps, can it be confidently asserted that in experience and heredity we have all the terms of the problem. The little we can say is, that though in the dark we need not consider ourselves more in the dark as to the origin of those strange instincts than we are concerning the origin of those wonderful organs of astonishing and exquisite mechanism that, especially among the insects, are the instruments of those instincts. Nay, more, if the view we have put forward

concerning the connection between mental manifestations and bodily organization be correct, the question of the origin of these mysterious instincts is not more difficult than, or different from, but is the same with, the problem of the origin of the physical structure of the creatures; for, however they may have come by their bodies, they cannot fail to have the minds that correspond thereto. When, as by a miracle, the lovely butterfly bursts from the chrysalis full-winged and perfect, and flutters off a thing of soft and gorgeous beauty, it but wakes to a higher life, to a new mode of existence, in which, strange though it may sound, it has, for the most part, nothing to learn, *because* its little life flows from its organization like melody from a music box. But we need not enlarge on this a second time.

In seeking to understand the phenomena of instinct we of course get the full benefit of the law of Natural Selection, which, though it throws no light on the origin of anything, mental or physical—for, as Mr. Darwin says, it “has no relation whatever to the primary cause of any modification of structure”—nevertheless helps us to understand the existence of instincts far removed from the circumstances or conditions of life under which they could have been acquired. Suppose a Robinson Crusoe to take, soon after his landing, a couple of parrots, and to teach them to say in very good English, “How do you do, sir?”—that the young of these birds are also taught by Mr. Crusoe and their parents to say, “How do you do, sir?”—and that Mr. Crusoe, having little else to do, sets to work to prove the doctrine of Inherited Association by direct experiment. He continues his teaching, and every year breeds from the birds of the last and previous years that say “How do you do, sir?” most frequently and with the best accent. After a sufficient number of generations his young parrots, continually hearing their parents and a hundred other birds saying “How do you do, sir?” begin to repeat these words so soon that an experiment is needed to decide whether it is by instinct or imitation; and perhaps it is part of both. Eventually, however, the instinct is established. And though now Mr. Crusoe dies, and leaves no record of his work, the instinct will not die, not for a long time at least; and if the parrots themselves have acquired a taste for good English the best speakers will be sexually selected, and the instinct will

certainly endure to astonish and perplex mankind, though in truth we may as well wonder at the crowing of the cock or the song of the skylark. Again, turkeys have an instinctive art of catching flies, which, it is manifest, the creatures in their present shape may have acquired by experience. But suppose the circumstances of their life to change; flies steadily become more abundant, and other kinds of food scarcer: the best fly-catchers are now the fittest to live, and each generation they are naturally selected. This process goes on, experience probably adding to the instinct in ways that we need to attempt to conceive, until a variety or species is produced that feeds on flies alone. To look at, this new bird will differ considerably from its turkey ancestors; for change in food and in habits of life will have affected its physical conformation, and every useful modification of structure will have been preserved by natural selection. My point however is, that thus, by no inconceivable steps, would be produced a race of birds depending for all their food on an instinctive art, which they, as then constituted, could never have acquired, because they never could have existed without it.

No doubt, to the many, who love more to gaze and marvel than to question and reflect, all this will seem miserably inadequate as a clue to one of the greatest mysteries of life. But enough, if I have indicated my view of how the most inexplicable of instincts may have had their origin; or rather, if I have shown how our utter inability to trace them back to their origin tells nothing against the probability that they all came into existence in accordance with those laws of acquisition and heredity that we now see operating before our eyes. We cannot tell how the pupa of the dragon-fly came by the instinct that prompts it to leave the water and hang itself up to dry. But we may be able to explain this quite as soon as to unveil the origin of the hooks by which it hangs itself up. And if ever human intelligence should so trace the evolution of living forms as to be able to say, “Thus was developed the bill-scale wherewith birds now break their way out of the shell,” it will probably be able to add, “and these were the experiences to which we must trace the instinct that makes every little bird its own skilful accoucheur.”

DOUGLAS A. SPALDING.

Is Modern Ethology Objective?

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Ethology is an old word, once used in a wide sense for behaviour in general or even more widely as almost synonymous with "bionomics." Recently it has become associated with one particular theory of behaviour, that due in the first place to Konrad Lorenz (1937a and b, 1950) and amended by N. Tinbergen (1942, 1950, 1951), G. P. Baerends (1941) and others. Behaviour students have now to choose between one or two courses: either attempting to restore the old broad use of the name ethology for the study of behaviour in general (there is no other single word for this); or relinquishing the name to Lorenz and his school. The latter course is chosen here, adding to Ethology the qualification "modern" to distinguish the new, restricted meaning of the term from its old broad one. Unless this distinction be made between the study of behaviour in which we are all engaged, and the particular approach to it which has taken over the name of Ethology, it will seem that this particular approach has become the agreed basis for work in this field. Yet the view point of modern Ethology is not generally accepted by members of the Association, and still less, probably, by potential members. In at least one University the same students have been given lectures both for and against the ethologists' approach to behaviour: it is a matter of lively controversy for which the Association provides the natural forum. The greatest service of ethologists to progress in this field may well turn out to be that they have engendered controversy.

Modern ethologists have carried out stimulating and often beautiful experiments, notably in the analysis of complex stimulus-situations. But there is no doubt that the main attraction of their approach lies in its claim to objectivity in a field, instinct, where objectivity has been conspicuous for its absence in the past. Many of us brought up more or less under the influence of "reflexological" theories of behaviour, with their Loeb-Kühn-Fraenkel-Gunn elaborations of taxes and kineses, experienced a certain sense of liberation on encountering the ideas of the modern ethologists. On closer examination however, what had seemed at first

sight perhaps minor defects in their theory, proved so serious as to invalidate entirely its claim to objectivity.

This may seem a surprising judgement. Tinbergen (1942, 1951) has set forth the scientific objections to teleology, anthropomorphism and subjectivism as cogently as any mechanist could ask. He even coined the word "objectivistic" to distinguish his approach. He deplores the "tenacious hold" of subjectivism on the study of behaviour, with its reliance on analogy and its anti-analytical consequences. What little published criticism there has been of modern ethology points the same way, the misgivings of many physiologists having remained unprinted. Thus Bierens de Haan (1947) took the ethologists to task for being too objective, and Thorpe (1948) expressed some sympathy with his point of view. Others like Schneirla (1952), Hebb (1953) and Armstrong (1950) have criticised particular aspects of ethological theory but have not gone so far as to question its objectivity, being all on the psychological rather than the physiological wing of the subject themselves. There has been one exception in this respect. It was Carthy (1951) who first pointed out that: "the central idea of the motivating force of reaction specific energy arising within the animal itself . . . is in many ways closely similar to ideas in psycho-analytical theory."

This was not an overstatement. It is true, as Carthy implies there, that the central idea in Lorenz's theory is not reaction-specific energy itself, although contained in it: the idea that the energy is specific is being discarded among ethologists themselves. The central idea is that there exists an endogenous, accumulable, consumable form of nervous energy as a distinct physiological category. Lorenz (1950) is quite explicit about this, stressing: "the peculiarity and independence of endogenous activity as a distinct physiological process." The answer to the question, distinct from what?, is also quite clear: distinct from reflex action. Whitman's and Heinroth's signal contribution was to discover, according to Lorenz, "an independent, particulate function of the central nervous

system which . . . is, at the very least, equally as important as the reflex." Internal energy accumulation, and external stimulation, are, he writes, "two absolutely heterogeneous causal factors."

It may be said that these formulations are deliberately extreme and need not be taken too literally. Ethological theory is open to revision and ethologists, by no means agreed on all points, are themselves busy revising it (as Bastock, Morris and Moynihan, 1953). One may perhaps look forward to eventual revision of Lorenz's central thesis itself. But so far his idea of two distinct neurophysiological processes, one internal, and one reflex, continues to provide the agreed basis for the whole school. In fact this idea will need more than revisions if ethology is to make good its claim to objectivity, because it is a subjective one.

Energy and Id

Ethology is subjectivist on its own showing, as a *dualist* theory. Ethological *energy*, conceived as absolutely distinct from reflex mechanisms which alone have direct external relations, is quite as subjective a concept as the Freudian *id*. It matters little whether the prime mover inside the animal is called a "biological need" or "purpose" or by other such explicitly subjective teleological names; or whether it is called "energy" or "potential" or "impulses" which have a neutral and even physiological sound. What matters is that all these are prime movers and inside and quite distinct from reflexes: that is what makes them subjective. That is to say they are all unwarranted analogies from man, in whose behaviour subjective phenomena, appearing to us as prime movers inside, do undoubtedly play some causal role. As Tinbergen (1951) says, even in man subjective phenomena are of very limited use for the causal analysis of behaviour.

The kinship between ethology and Freud which Carthy pointed out lies in their dualism. How closely the two theories approximate should be more generally known, because many zoologists might at first hardly credit the fact that what Lorenz has managed to do is to win wide acceptance among zoologists for the wholly subjective concepts of psychoanalysis. There are of course differences between Lorenz's and Freud's theories, the most important being that Freud admitted only two basic instincts and made no attempts to compromise with physiology. But here are some

passages from Freud's final summing up of his theory:

"The core of our being is formed by the obscure *id* which has no direct relations with the external world . . ."

"It contains everything that is inherited, that is present at birth, that is fixed in the constitution—above all, therefore, the instincts . . ."

"The power of the *id* expresses the true purpose of the individual organism's life. This consists in the satisfaction of its innate needs . . . The forces which we assume to exist behind the tensions caused by the needs of the *id* are called *instincts* . . ."

"We have found that the instincts can change their aim (by displacement) and also that they can replace one another—the energy of one instinct passing over to another." (Freud, 1949, pp. 2, 5 and 67).

The working ideas of ethology are there in a body: purpose as satisfaction, tensions, fixity, innateness, separation from the external world; even energy, and its displacement between instincts; and even, one cannot but add, to the obscurity at the core. Further, the separate "coat of reflexes"—the ethological term borrowed from von Holst—which regulates the discharge of energy in relation to the external situation, corresponds (despite its physiological flavour) with Freud's *ego*: "a special organisation which acts as an intermediary between the *id* and the external world" (Freud, 1949). Thus Lorenz and Freud both draw a distinction in principle between the nervous machine and its motor, between reflex action and the energy for action.

This idea was not of course original with Freud, who acknowledged the priority of Empedocles. Empedocles made a separation in principle between the four material Elements (earth, air, fire and water) on the one side, and on the other, the two forces (love and hate) which alone moved the material elements. Empedocles's dualism has been abandoned in modern physics and chemistry, along with his short list of four elements. It is only in biology, psychology, philosophy and related fields, that dualism remains a strong current, apparently for social reasons. In general biology such dualism is of course called Vitalism. In the particular field of behaviour, as Lorenz (1950) takes some trouble to point out, vitalism typically appears as subjectivism. But the link between *dualism* and vitalism he seems to have missed. He seems not to notice that in transferring back to animals the sort of dualism which Descartes restricted to man, he is re-creating a vitalist, subjective theory of animal behaviour (see also Kennedy, 1954).

What is at first sight so confusing about ethology, until one examines its dualist foundation, is that Lorenz places himself firmly on the side of mechanism against vitalism. He regards "the reciprocal errors of the mechanists' reactions as justified in themselves and erring only through exaggeration" (Lorenz, 1950). That is the position of a great many experimental zoologists. It is true, as Thorpe (1953) says, that the idea of instinct has in general been highly repugnant to them. It is also true as Lorenz (1950) says, that this was due partly to the great stress vitalists laid upon instinct. The endeavour of mechanists has been therefore not so much to explain, as to explain away instinct. It is the bold bid of ethology to save mechanism from its friends, the earlier mechanists, whose "grotesque simplifications" (Tinbergen) played into the hands of the vitalists, although the latter were "much more fundamentally wrong" (Lorenz). The vitalist essence of ethological theory is thus far from being the most obvious thing about it.

According to the vitalists, Lorenz (1950) writes, spontaneous activity must be purposive and therefore variable; according to the earlier mechanists, such fixed innate behaviour patterns are reflex chains and must therefore be "totally devoid of spontaneity . . . But on closer inspection it became apparent that these activities are, at bottom, to a very high degree independent of external stimulation." Even a very high degree of independence is not of course the same thing as an absolute separation, such as ethologists make on this kind of evidence. Even *vacuum activity* has not been shown to be absolutely spontaneous no matter how "irrelevant" it may be. An animal achieves absolute independence of external stimulation when it dies. In other contexts ethologists are ready enough to grant the flow of *energy* from one part of the nervous system to another, in the functioning of *hierarchies* and *displacement reactions*. This immediately opens the possibility (to non-ethologists, the certainty) of past and present external stimulation being reflected in a variety of activities according to the circumstances, and not merely in the single one with which the given type of stimulation is most immediately connected—and that only in an excitatory capacity—in the nervous system. The task is to work out the laws governing these complex events. But in this context, ethologists confine our attention to one kind of immediate stimulation, the one typically "releasing" the

given response, and, showing that it can be virtually imperceptible, proceed to set up an absolute distinction between external stimulation and endogenous activity.

Reflexes and Instincts

The second point in support of the claim that modern ethology is not objective but subjective, is connected with the first, but concerns reflexes. Ethologists have effectively disposed of the old "reflexological," "telephone-exchange" theory that behaviour consists of a sum of fixed reflexes. What they call the "priming" of reactions does occur as well as their immediate elicitation by particular external stimuli. The sharp distinction they make between these two processes of priming and release, fundamental to the theory, rests, however, on a conception of the reflex as rigid and old-fashioned as that of the reflexologists they justly criticize. Instead of going forward from the criticism of reflexology to build upon modern reflex physiology (a very different thing) they curiously ignore key parts of it. They retain the discredited picture of the telephone-exchange reflex, merely limiting its occurrence and making this very limitation the grounds for postulating nervous processes which are not reflex at all.

It is most difficult to see what, other than the subjectivism at the root of ethological theory, can explain this. For in reality there is neither need nor room for a separate category of central nervous process to set against and complement the reflex. Physiologically considered, the change in the excitatory state of a neurone or centre is not something distinct from, but an integral part of every reaction no matter how simple. This is what Creed, Denny-Brown, Eccles, Liddell and Sherrington (1932) have to say about it in their book: "*the motor centre even at its spinal simplest is more than a passive relay forwarding impulses on their way out to their muscle.*" For physiologists, the excitatory state of a centre is determined not by some peculiar, independent process inside it, but, on the contrary, by outside influence upon it.

"Under intact natural conditions we have to think of each motoneurone as a convergence-point about which summate not only the excitation processes fed by converging impulses of varying provenance arriving by various routes, but also inhibitory influences of varied provenance and path: and that there at that convergence-point these two opposing processes finally interact . . . Whether the excitatory has the upper hand, or whether the inhibitory, commonly both are at work, and the functional state of the motoneurone indexes the net result from the two," (*ibid.*)

There is no room here for any distinction in principle between endogenous and exogenous stimuli in their mode of action at the motor centre. But there is plenty of room, in view of the multitudinous connections of every neurone with others, for ordered variation in the effectiveness of any one type of peripheral stimulus in bringing about or preventing motor discharge.

It is a not unreasonable complaint of behaviour students that physiology has helped them disappointingly little. But whatever the physiologists have failed so far to do they have as a body provided the firmest possible ground for Pavlov's (1928) contention that "there is no essential difference between the two phenomena designated as reflex and as instinct."

"When one considers," he went on, "that any given reflex, as a response to certain external conditions, is not only governed and regulated by other simultaneous reflex actions, but also by a multitude of internal reflexes as well as by the presence of many internal stimuli, chemical, thermal, etc., operating in different regions of the central nervous system or even in the executive elements (motor and secretory), then such a conception would include as reflexes the entire complexity of all responsive reactions, and nothing would remain to necessitate the forming of a special group of phenomena known as instincts."

In attributing the crudely "reflexological" view of behaviour to Pavlov, ethologists are very wide of the mark; and what is more important, having justly criticized that erroneous view, they put an even less scientific one in its place. Pavlov preferred the term *reflex* to *instinct*, not because he was a "reflexologist" but because *reflex* had "had from the beginning a purely scientific connotation," embodying as it does "the principle of determinism." Ethologists would readily agree that that is more than can be said for *instinct*. Pavlov did not of course devote himself to the study of unconditioned reflexes, although some of the laws he established are directly applicable to innate behaviour. He was aware of this omission and said that the study of instincts was the "next important task" (Pavlov, 1928, p. 296). Due credit goes to the ethologists for putting this task again in the foreground for us and for removing some of the theoretical obstacles that have delayed the attack on it. It is certainly very hard, however, to tackle this problem and still keep one's feet firmly on the physiological ground.

By what means did ethologists succeed in

directing renewed experimental attention to innate behaviour? They did so by emphasising how much of the variation in behaviour might be due to the working of the innate part of the system without, necessarily, the intervention of conditioning processes. This had previously been effectively obscured by views of instinct as either rigid, or if not rigid, then "intelligent" (Thorpe, 1948). The ordered variation of instinctive behaviour is the significant objective point underlying (although misleadingly conveyed by) Wallace Craig's distinction between *appetitive behaviour* and *consummatory act* (or *fixed pattern*), Lorenz's distinction between *Taxiskomponent* and *Erkoordination*, and Tinbergen's hierarchy of *moods*.

Having once recognized that ordered variation is a property not only of learned but also of instinctive behaviour, the logical next task is surely to study the interaction of these two kinds of variation in the animal. For comparative ethologists, great interest would attach to the detailed analysis of evolutionary differences in the relative importance of the two—the degree of dominance of conditioned over unconditioned reflexes—as one passes through the animal kingdom, from worms to insects, fishes to birds, mammals to man. It is another point in support of the claim that ethology is still not an objective theory, that this is not yet the sort of programme ethologists set themselves. For they cannot yet consolidate the advance they have made, and even endanger it, because of their tendency to force into the portmanteau of instinct as much of the variation in behaviour as they possibly can. This tendency is the inevitable result of the subjectivist separation of a motivating core from a reflex coat in the causation of behaviour. Given that separation, conditioned reflexes are tacitly excluded from a direct part in changing "motivation." That was the evident logic behind Tinbergen's (1951) programme of studying instinctive behaviour first, and learned behaviour only afterwards. Hebb (1953) has well brought out the impracticability of this. If in fact instincts and simpler reflexes differ only in degree (although Hebb does not make that point), then instinctive and learned behaviour must become an "inextricable tangle" as Hebb put it, and there is plenty of evidence that they do. What this means, unfortunately, is that the whole ethological interpretation of stickleback behaviour, for example, will have to be revised

and much experimental work done over again.

Today, it would be most rash to set any *a priori* limits to the extent to which conditioned reflexes intervene in the very processes which ethologists have treated as non-reflex, innate and endogenous. Hebb understated the case when he wrote: "there is no behaviour, beyond the level of the reflex, that is not essentially dependent on learning." No such level can be distinguished physiologically. The reflex cannot be used to mark a level; its value is rather that it characterizes the elementary mode of operation of the nervous system at all levels. The contraction of the human pupil in response to light is not merely a reflex but an autonomic one, yet Hudgins (1933) conditioned it and, by stages of conditioning, actually made it voluntary. Vasomotor responses, again, have been conditioned (Menzies, 1937; Gottschalk, 1946), although they enter into emotion which Lorenz (1950) correlated solely with endogenous energy discharge. Especially pertinent is the work of Bykov (1938, 1953) and his school on more strictly "internal" factors (ethologically speaking) than these classical reflexes. Among the internal factors cited by ethologists, hormones loom large. Hormone action might seem at any rate a good deal more innate than, say, salivation at the sound of a bell. Nevertheless it and many other visceral functions have been conditioned.

Injections of adrenaline into dogs, in one experiment, were repeatedly accompanied by the sound of a bell, and produced the usual effects of this hormone including rise of blood pressure and pulse rate. After a while the bell alone produced the same effects. Then, even when the sound of the bell was accompanied instead by an injection of acetyl-choline under conditions in which it would normally produce the opposite effects (fall of blood pressure, etc.), the effects of the bell and injection were nevertheless the same as they had been with adrenaline. Thus conditioned reflexes may have more "energy" than unconditioned. The resting metabolic rate, another profoundly "internal" factor which undoubtedly primes many reactions, has also been experimentally conditioned by these workers. As a result of conditioning, the mere sight of particular surroundings where physical work has habitually been done, or merely assuming a posture in which heat loss has habitually had to be compensated, may lead to a rise of metabolic rate. It would be rather surprising if conditioning

played no comparable part at all in the territorial behaviour of sticklebacks.

The diuretic activity of the kidneys of dogs has also been conditioned (Bykov & Alexeyev-Berkmann, 1930; Bykov, 1938; Marx, 1931)—an irresistible example to quote, inasmuch as the resultant filling of the bladder is what primes the instinctive act of micturition; Lorenz could have found here a living model for his scheme. And in the living model, it is seen that the two processes of priming (bladder-filling) and of release (by, say, lamp-post) are neither absolutely nor innately distinct. Both are in principle reflex, and become partially separated only as the animal grows up. Many conditioned reflexes of the reciprocal type have also been elaborated, where some visceral change, as of stomach contents or blood composition, has been used as the conditioning *stimulus*. Finally it might be mentioned that the alpha rhythm in the cerebral cortex (in any case notoriously sensitive to environmental conditions) is also profoundly affected by conditioning processes.

It seems clear that in an animal like a dog, all reflexes from the simplest up to elaborate instincts are under cortical control, meaning that their performance depends upon the formation and extinction of conditioned reflexes from the internal and external world. It is a very far cry from the old rigid "reflexological" picture of the reflex to the modern picture these workers are slowly constructing. They think in terms of reflex-complexes: on the basis of the instinctive systems of unconditioned reflexes (some of which show some conditioned reflex properties) there are built whole systems of conditioned reflexes which themselves show a certain stereotypy and independence one from another. Here again all workers in the field of behaviour are faced with a choice: given that the old picture of the reflex was a wooden caricature of reality, whether drastically to restrict the term or even drop it entirely, or whether to try and modernize it. Ethologists have chosen to restrict it, Pavlovians to modernize it. Unfortunately, so restricting the term deprives it of physiological meaning, while abandoning it altogether incurs still greater risks. It is extremely hard to break what Tinbergen so justly called the tenacious hold of subjectivism on behaviour. That is why we can hardly afford to follow him in rejecting the "reflex hypothesis" of behaviour. When that goes out of the door, subjectivism flies in at the window.

Cost of Subjectivism

Only subjectivism, with its pre-occupation with the ends of behaviour sequences, can surely explain, for example, Tinbergen's assumption that migration in the stickleback is motivated by a top *reproductive* centre. Spurway and Haldane (1953) have recently pointed out that another cause of migration is more probable. Tinbergen's view that the connection between migration and reproduction must be *central*, with the second *internally* exciting the first, was an *a priori* one, based on little but the fact that reproduction is normally the ultimate consequence of migration. The advantage of a broadly reflex theory of behaviour here is that it guides the investigator to the efficient causes of sequences or hierarchies of behaviour. In so far as such sequences do lead to a particular, useful end, the causes lie in the occurrence in normal sequence of the environmental conditions to which the animals respond, the responses having become suitably adapted during evolution.

Passing to the other end of the ethological hierarchy, it again seems to require the tenacious hold of subjectivism to explain why ethological workers (Bastock, Morris and Moynihan, 1953) are only now groping toward the physiologically self-evident fact that what causes the sharp change of behaviour after a *consummatory act* is not the consumption or running out of impulses (real nerve impulses do not do that sort of thing), but to an input of impulses from the periphery. The change in behaviour at this point reflects the input: it is reflex. One other point must suffice to show how little real change has been effected by Tinbergen's replacement of the earlier ethological term *energy* by a more physiological one, *impulse*. These ethological ("motivating") impulses, quite unlike physiological ones, are never inhibitory but always excitatory. This discrepancy is so plain that ethological theory will no doubt in due course be amended accordingly. The point is that it need never have occurred if the theory had not been subjectivist; and until the theory ceases to be subjectivist, such amendments will continue to provide an unnecessary labour for ethologists.

The ethological treatment of *displacement reactions* also suffers from subjectivism. Considered taxonomically, the displacement of a response from one reaction chain to another in the course of evolution is a clear and useful idea, suggesting a change in central nervous

connections. Ethological work on this subject including the "ritualized" modification of such elements and their morphological complements in the new context, is a stimulating development (Baerends, 1950). But the concept of displacement is again directly applied, by unwarranted analogy, to the causal explanation of the behaviour. Any response that turns up in the chain but is biologically "irrelevant" or displaced, is by the same token explained as physiologically "displaced." Tinbergen (1951) says it does not "belong to the motor pattern of the instinct activated," on his assumption that "all the activities forming part of a purposive behaviour pattern aimed at a certain goal depend on a common neuro-physiological pattern." Evolutionary and physiological causes are confused here in just the way Tinbergen elsewhere says they should not be. The idea that responses properly belong to one or other instinctive reaction chain, depends absolutely on the subjective notion that every chain is internally directed to its one normally-observed end by impulses from a nervous centre or pattern "for" that end. Physiologically considered, displacement appears to be a special case of *positive induction*. It looks very much like the central excitation of a third reflex as a result of two others which are mutually inhibitory, both being externally excited at the same time: for example, fighting and fleeing. Analysis on such lines must be hampered, however, by a theory which attributes displacement to a conflict between internal forces called drives which are labelled, as if caused, by their ends.

Finally, something should be said of the ethologists' repeated use of subjective terms such as purpose, drive, mood, appetite, consummation, and so on. Ethologists agree that these terms were used impermissibly subjectively before, but now use them freely. It is a matter of importance to enquire whether adequate reasons for doing so have been brought forward; for if not, then the use of these terms is open to all the old objections Tinbergen (1951) enumerates, and is alone strong evidence of the subjectivism of ethology itself.

These terms came to acquire their new respectability for ethologists, originally, on the strength of Wallace Craig's scheme of instinctive behaviour, at a time when *energy* was supposed to be strictly action-specific. The scheme comprised three parts, set out thus by Lorenz

(1950; see also Thorpe, 1948):

- (1) accumulation of action-specific energy giving rise to appetitive behaviour;
- (2) appetitive behaviour striving for and attaining the stimulus situation activating the innate releasing mechanism;
- (3) setting off the releasing mechanism and discharge of endogenous activity in a consummatory action.

It was by treating this sequence as if it were not only a coloured description of the observed sequence of behaviour, but was also, by direct analogy, a description of the underlying physiological process, that the old subjective terms acquired their new objectivist legitimacy. If the centre for an innate behaviour pattern or "endogenous movement"—an act which appeared *overtly* only at the end of a long behaviour sequence—if that centre were also the source of all the activity preceding the final act, then, it seemed that here was an objective physiological basis for previously subjective concepts like purpose and consummation. As Lorenz (1950) put it, "though the activities thus elicited comprise the whole range of behaviour, they have one decisive characteristic in common: they are all *purposive* in the sense which E. C. Tolman has given to this term, that is to say, they all tend to bring about, by *variable* movements, an invariable end or goal."

But did Wallace Craig's tripartite scheme provide an objective basis for the previously subjective terms, or was it the subjective ideas that created the tripartite scheme? It is difficult to accept the claim that the terms ever became objective, when they continue to be used even after their objective basis, the tripartite scheme, has been abandoned as the general case. It is now agreed, thanks to Baerends, by Lorenz and Tinbergen that ends as well as means may be variable. The behaviour leading normally to a certain end-action is not now held to be caused by the centre of that end-action itself, but from a different, higher centre instead. It is now agreed that which one, out of a number of possible *consummatory acts*, actually occurs, depends upon what external stimuli are received. One might therefore have expected that the idea of behaviour being directed internally, (whether by a stream of "motivating impulses" or otherwise), might have been abandoned too, along with terms based on it like purpose, drive, consummation and so on.

That these terms are retained even temporarily; can only be explained by the tenacious hold of subjectivism. It is the basic subjectivist assumption that behaviour sequences must be caused by parallel, counterpart, internal connections that has to be abandoned ultimately. When it is abandoned, it will be seen that the ordered variation both of instinctive behaviour, and that due to conditioning, serve the single function of the nervous system as defined by J. E. Smith (1950): "to take appraisal of environmental changes, and to promote responses which lead to favourable adjustments." It need hardly be added that once ethologists come round to this, their peculiar assets—experimental skill, and especially their determination to tackle the long-neglected higher functions of the intact nervous system—can be turned to enormous advantage.

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An Apparatus for Analysing the Pattern of Spontaneous Activity in Laboratory Animals

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Much of the activity of the laboratory animal is spontaneous in the sense that it consists of running which does not seem to be related either to well-defined stimuli or to any clear goal. On the other hand the initiation of running, its rate of performance and its subsequent arrest are presumably controlled by the interaction of cerebral centres which are brought to the appropriate degree of facilitation by external stimuli acting through the sense organs, by nervous influences from other parts of the brain, and by changes in the constitution of internal environment. An example of the effect of disturbing the normal inter-relationship between cerebral centres is seen in the considerable increase in the volume of undirected activity which follows injury to the orbito-frontal cortex (Richter & Hawkes, 1939). It does not follow, however, that other factors such as the sex hormones, which produce an apparently similar effect, do so by their action on the same centres, for the total volume of activity alone provides too little evidence to warrant such a conclusion.

In a considerable literature dealing with the measurement of this type of activity and the factors which influence it emphasis has, for the most part, been laid on the total amount of running taking place during a given time (see Munn, 1950). More detailed information may be obtained by examining the components of spontaneous activity (such as the speed of locomotion, its frequency of occurrence and its duration) and the changes in each of these components which characterise the application of various experimental procedures.

The pattern of spontaneous activity of an animal may conveniently be defined in quantitative terms by the following characteristics:

- (i) the distance run each 24 hours,
- (ii) the length of time given up to running in each 24 hours,
- (iii) the distribution within each 24 hours of the distance run,

- (iv) the distribution of the time spent in running, and, by comparing (iii) and (iv),
- (v) the velocity of running and its temporal distribution.

This paper describes an apparatus which is being used to measure these parameters.

Principle of Construction

The apparatus which is illustrated in Figs. 1 and 2 is suitable for use in conjunction with living cages in which the volume of activity of the animal can be directly related to the "make and break" of an electric circuit. Suitable arrangements of living accommodation have been described elsewhere (Eayrs, 1951, 1954). When an animal moves in such a cage an electric circuit is made and broken, each interruption being recorded on an electro-magnetic register. The difference between two successive readings of the register thus gives an estimate of the total amount of activity taking place during the intervening period, normally 24 hours. The "make and break" of the circuit also causes a pointer to write on a kymograph revolving at a slow and constant speed (about once in 24 hours). As a result the record obtained in this way shows both the length of time the rat was engaged in locomotor activity and the distribution of this activity throughout each 24 hour period. Simultaneously, the interruptions to the circuit are recorded by an additional instrument designed to facilitate the quantitative analysis of the total amount of activity into hourly components. The constituent parts of the apparatus are described in the following paragraphs.

(a) Unit Registering Total Activity

The mode of assembly of the unit operating the electro-magnetic registers is illustrated in Fig. 1(b) where, for simplicity, only the power source and the components associated with one activity cage are given. The power is derived from a mains operated transformer giving, after rectification, D.C. voltages of 6 v. and 50 v.

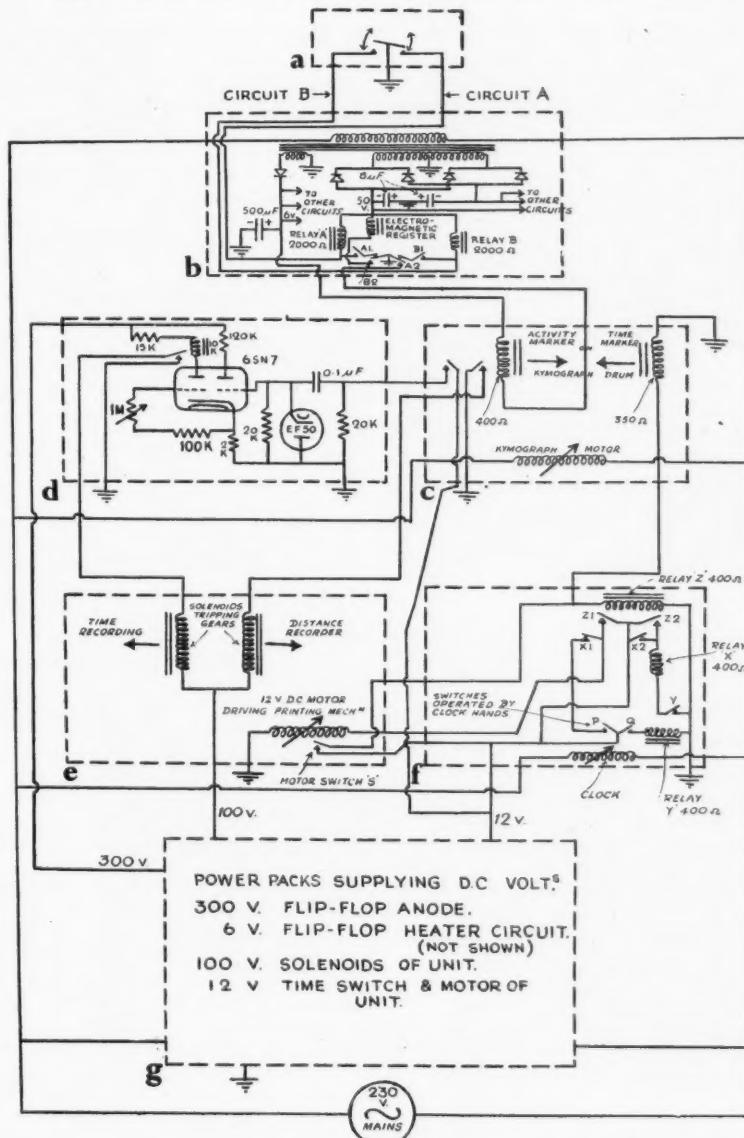


Fig. 1. Activity recording apparatus: Circuit diagram linking up the constituent parts. The dotted lines surround the assemblies which can be identified on Fig. 2.

- (a) Switches associated with living cage.
- (b) Unit registering total activity.
- (c) Unit recording duration of activity.
- (d) Flip-flop.
- (e) Unit analysing distribution of activity.
- (f) Time switch.
- (g) Power pack.

The 50 v. power source is used to activate a system of electro-magnetic relays designed to prevent any small oscillating motion about a single "make and break" contact from being recorded as locomotor activity. For example, completion of circuit A (activating relay A) causes switch A1 to close and so complete a subsidiary self-holding circuit. No further activity can be recorded by this circuit until the movement of the animal in its cage completes circuit B. When this occurs relay B is activated closing switch B1 and holding relay B magnetised, while at the same time opening switch B2. The self-holding circuit for relay A is thus broken and switch A1 returns to its original position. No further activity can now be recorded from the contact associated with relay B until the animal's activity remakes circuit A.

Every time that relay B is activated, a circuit is made through switch B2 which energises an electro-magnetic register with the change of one digit. Re-activation of relay A resets the register and at the same time completes, through switch A2, a further circuit involving the 6 v. power source. This activates the marker on the kymograph drum which records the duration of activity.

(b) *Unit Recording the Hour-by-hour Duration of Activity (Fig. 1(c))*

The apparatus used to record the hourly distribution of activity within each period of 24 hours consists of a kymograph turning one revolution in just over 24 hours, which is provided with an electrically operated marker for each activity cage. Each marker consists of a balsa-wood and celluloid pointer glued to the hinged arm of a 400Ω electro-magnetic relay (two "make and break" switches). The relays are energised by the 6 v. power source described in the previous section, so that the pointer writes on the drum in a downward direction every time circuit A is activated and returns to its original position when circuit B is completed. The kymograph is also provided with a time marker activated hourly in a manner which is described below.

(c) *Unit Analysing the Distribution of Activity*

Although the kymograph trace gives a good visual record of the diurnal distribution of activity such a record is not easy to measure. In the first place, individual marks tend to merge together during bursts of considerable activity and therefore cannot be counted.

Secondly, when activity is made up of a large number of short bursts, measurement of its duration is less precise than that of a small number of long bursts. To overcome these difficulties an instrument designed to reduce the number of measurements to one for each hour (or such other unit of time as may be chosen) is incorporated in the apparatus. This instrument, illustrated in Figs. 1(e) and 3, consists of paired solenoids, each of which is arranged to operate a ratchet and pinion by means of a hinged lever. Each time the solenoid is energised the movement of the lever and ratchet causes a pinion to rotate through one tooth. This rotation is transmitted through a chain of gears in such a way that a thread of catgut is caused to wind round a bobbin mounted at one end of the instrument. This draws a slide along a guide slot through a distance which is proportional to the volume of activity of the animal.

One of each pair of solenoids is activated by one of the two make and break switches incorporated in the electro-magnetic relay which marks the kymograph drum. The slide driven by this solenoid therefore travels a distance which is directly proportional to that run by the animal. The other solenoid of the pair is simultaneously activated, but in this instance a flip-flop (Fig. 1(d)) imposing a 3-second delay is incorporated into the circuit. The distance travelled by the slide drawn by this solenoid is therefore proportional to the length of time (in 3 second units) during which the animal was active.

A sharp-pointed pin is attached to the under surface of each slide and the position of these pins is printed hourly on to a piece of cartridge paper carried on a cork inlaid tray located underneath the framework holding the slides. To make this possible, the platform holding the tray is driven upwards by six reciprocally arranged cams driven by a 12 v. D.C. electric motor working through a chain of gears (reduction 513 x). Once the paper is pierced by the pins, the platform returns to its original position. In order that each pin shall make a new and readily identifiable pinhole every hour, even when no activity takes place during the preceding hour, the tray is automatically caused to move sideways a distance of about 1 mm. each time the platform rises and falls.

PLATE I

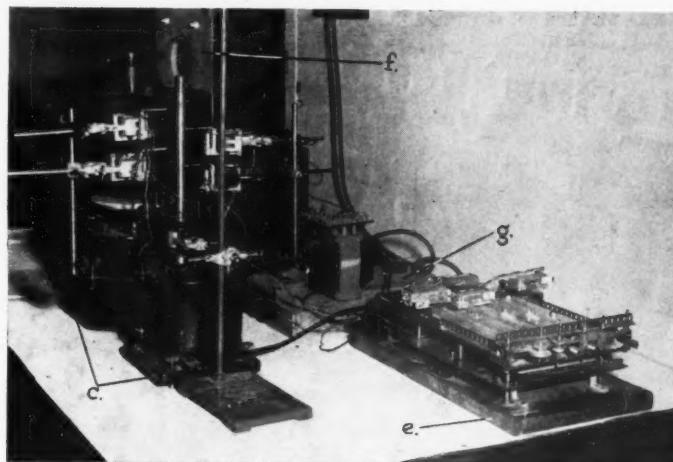
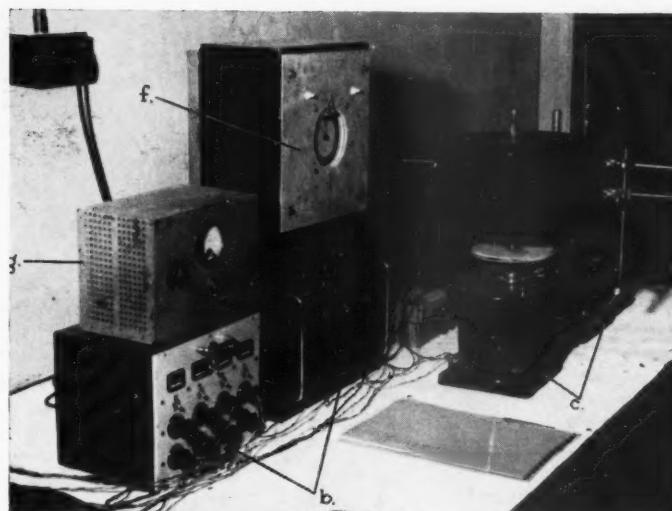


Fig. 2. The assembled activity recording apparatus. Lettering as in Fig. 1.

(Brit. J. anim. Behav., 2, 20-24)

PLATE II

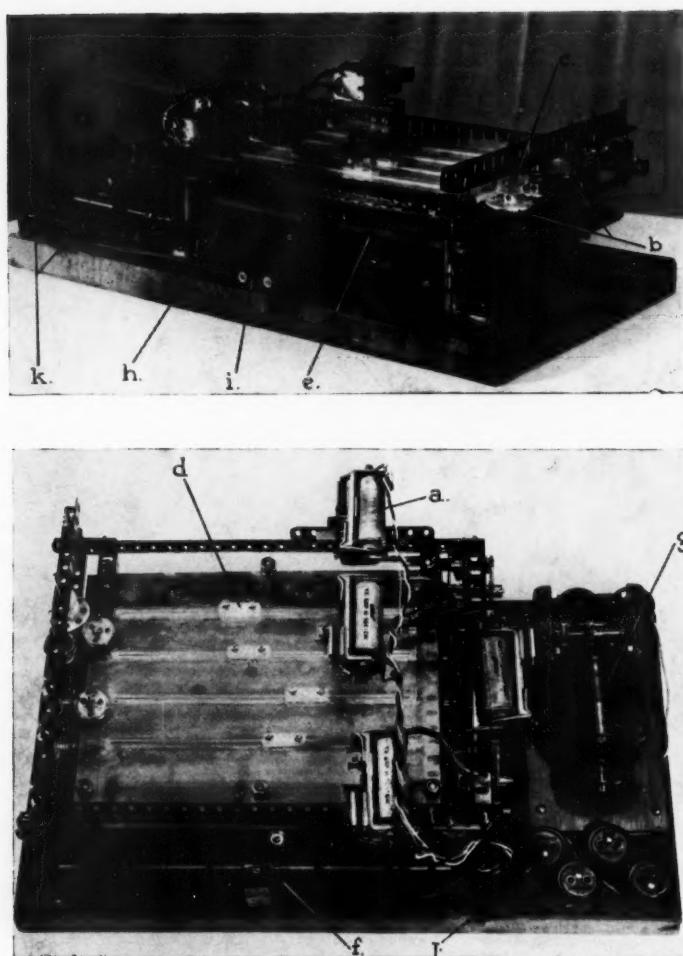


Fig. 3. Unit for analysing the distribution of activity during each 24 hours. Elevations showing mode of construction (see text).

- (a) Solenoid with tripping lever.
- (b) Gear trains driving bobbins.
- (c) Bobbin winding nylon thread.
- (d) Slide with pin undermounted.
- (e) Cork board holding cartridge paper.
- (f) Ratchet pinion and axle for drawing cork board transversely by means of nylon thread.
- (g) Electric motor and reduction gears for lifting platform (h).
- (h) Platform lifted by cams (not visible).
- (i) Switch S (see Fig. 1).
- (j) Sockets for electrical connections with activity recording switches.
- (k) Sockets for connections with electric motor.

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(d) Time Switch

An hourly timing mechanism is included to switch on the electric motor driving this unit and to switch it off after the platform has risen and fallen once only. The switch (Figs. 1(f) and 2) consists of an electric clock (mains 230 v. A.C.) whose face has been fitted with two brass contacts set 5 minutes apart. The centre of the minute hand is wired to the positive pole of a 12 v. D.C. power source and the sweep of the tip of the hand across the two contacts is equivalent to making and breaking switches P and Q in the circuit diagram of Fig. 1(f). When switch P is closed a circuit is made through switch X1, the electric motor starts up, and the platform begins to rise. This closes switch S (which is attached to the baseplate of the distance recording unit and is activated by the platform—see Fig. 3 i.), energising relay Z and closing switch Z1, thus completing a self-holding circuit which enables the motor to run independently of switch P. The activation of relay Z closes switch Z2, and so energises relay X. This causes

switch X2 to close (holding relay X) and switch X1 to open, cutting the motor circuit through switch P (the clock minute hand). The motor continues to run (through switch Z1) until the platform descends and opens switch S, breaking the circuit which is energising relay Z. Switches Z1 and Z2 therefore open, the former stopping the motor and the latter breaking the initial circuit activating relay X which however continues to hold through switch Z2. As long as this is the case the time switch is inert. It is reset when the

minute hand of the clock closes switch Z. This energises relay X, opening switch Y. The circuit through relay X is thus broken, and switch X1 closes. When the minute hand has passed over the second contact switch Q is opened and the cycle can thus be repeated about 55 minutes later when the minute hand again closes switch P.

The time-marker writing on the smoked kymograph drum of the unit recording the duration of activity is placed in parallel with relay Z, so that the closure of switch S ensures that a time mark is placed on the trace each time the printing mechanism of the instrument analysing the distribution of activity is operated.

Interpretation of the Records

The total distance run by each animal during a given interval of time is given by the difference between two consecutive readings of the appropriate electro-magnetic register. This can readily be converted into the actual distance covered, in yards. A visual picture of the pattern of this

activity is given by the kymograph trace, an example of which is illustrated by Figure 4(a). This can be expressed in quantitative terms by measuring the two associated records printed by the instrument analysing the distribution of activity. Examples of these records covering activity during 24 hours, are given

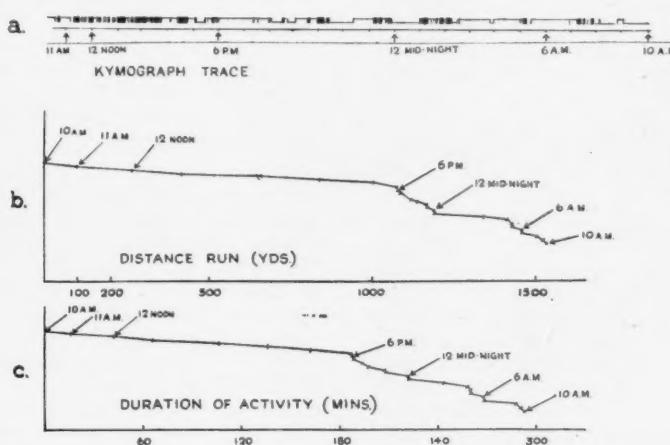


Fig. 4. Records of activity of male rat in activity wheel following treatment with DFP. For explanation see text. In figs. (b) and (c) the pinholes have been joined with solid lines to facilitate reading, and distance and time scales added.

in Figs. 4(b) and (c). In Fig. 4(b), which analyses the distance run into hourly components, the interval between the first and last marks is directly related to the total distance run by the animal (in this case the difference between

register readings represented 1551 yards). Each intervening mark can be identified with a given hour of the day, and the distance between these marks is proportionally related to the distance run by the animal each hour, which can therefore be calculated. Fig. 4(c) is the corresponding record which analyses the length of time spent by the rat in running the recorded distances. In this record the distance between the first and last marks measures the total number of 3-second periods during which the animal was active. The actual number can be assessed from the gear ratios of the driving mechanisms, and this number can be broken down into hourly components by measuring the distances between the intervening marks. The velocity of running each hour emerges as the ratio of the measurements made from Figs. 4(b) and (c) respectively.

Summary

An apparatus is described which has been designed to analyse the spontaneous activity

of small laboratory animals into the following components: the distance run, hour by hour; the proportion of each hour spent in running; and the velocity of running.

This apparatus can readily be modified to analyse activity into shorter or longer intervals than one hour.

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Spontaneous Activity in the Rat

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Internally motivated behaviour may, for convenience of description, be divided into two components: specifically directed or goal seeking behaviour such as nest building, copulation, and retrieving; and locomotor activity which apparently is of spontaneous origin. In the former, the evoking stimulus is usually well defined and the response follows a stereotyped pattern which ceases once the goal has been attained. On the other hand, 'spontaneous' or 'general' activity has no obvious goal and is set in motion by stimuli which are relatively ill-determined. This apparently random behaviour is however cyclical (Richter, 1922) and its extent is modified by a wide variety of environmental conditions, such as illumination (Browman, 1937), temperature (Browman, 1943) hunger and thirst (Richter, 1927), age (Shirley, 1928), sex (Hitchcock, 1925), endocrine influences (Richter, 1933, 1952), cortical ablation (Richter & Hawkes, 1939; Beach, 1941), the administration of drugs such as alcohol (Richter, 1926), amphetamine and caffeine (Tainter, 1943) and the presence of other animals (Durrant, 1935).

Two kinds of apparatus have been used to show the way in which these factors modify spontaneous activity: the stabilimeter cage and the revolving wheel or drum. In the first of these, the movement of an animal causes its living cage to rock or tilt and this motion has been recorded by both mechanical (Richter, 1927; Smith, 1940; Bousfield and Mote, 1943; Wilbur, 1936) or electronic (Campbell & McLean, 1948) devices. This type of cage is suitable for measuring the periodicity and duration of spontaneous activity, but in its usual form, it gives no information about the distance run by an animal. The activity wheel (Slonaker, 1908; Skinner, 1933) or table (Farris, 1941) on the other hand, measures distance but is inconvenient for estimating short period variations in the amount of activity. The fact that considerations of convenience seem to have governed the choice of technique implies that both types of apparatus are believed to measure the same thing, but no attempt has so

far been made to show whether this is the case. Munn (1950) suggests that it may not be so, and this likelihood has received experimental support from observations on the diurnal activity of normal and blinded lactating rats (Eayrs, 1951).

The present paper describes an experiment designed to study how far the characteristics of spontaneous activity depend upon the technique used to measure them.

Materials and Methods

Apparatus

For this study, four specially constructed stabilimeter cages and four revolving drums were used side by side. These were linked to an electrically operated recording system, described elsewhere (Eayrs, 1954) which registers the "make and break" of two integrated circuits to give permanent records of the amount and distribution of the activity taking place in each cage.

The stabilimeter cages, henceforward designated activity "galleries," are illustrated in Fig. 1. They consist of a wire mesh tunnel (A), 30" in diameter, which is attached to a circular platform (B) supported by a central pivot (C). Movement of the rat in the gallery causes a brass ring (D), which is fixed to the edge of the platform and is in electrical connection with the pivot (C), to roll over a series of brass contacts set flush with the surface of the bakelite base plate (E). Alternate contacts are wired together to form with the recording mechanism two independent circuits, one of which is completed each time the ring (D) rides on to a brass contact. Containers are fixed to the perimeter of the gallery at 120° intervals. Two of these are used to supply food and water, and the third holds a bottle which contains sufficient water to compensate for the weight of the food and drinking water. A tray (F) containing sawdust is fixed to the baseplate underneath the gallery to catch the faeces. The gallery is accurately counterbalanced by adding suitable amounts of mercury to each of four small specimen jars (G) which are sus-

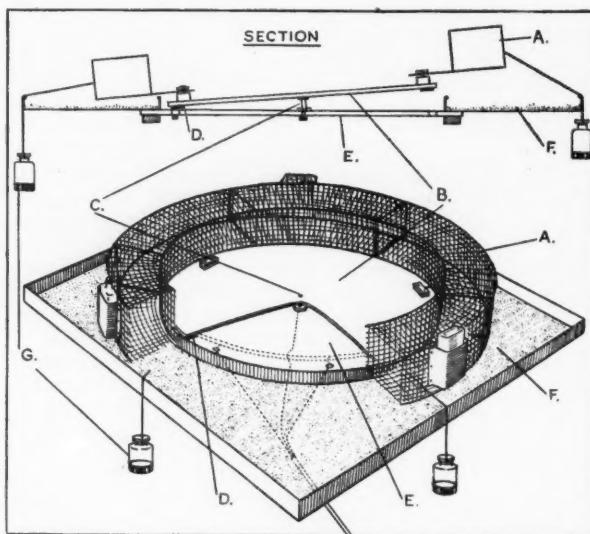


Fig. 1. Construction of activity gallery. For lettering see text.

pended from the gallery at 90° intervals. Adequate damping of the movement of the gallery is provided by the friction of the cords holding these bottles as they slide over the edge of the tray (F).

Except for two modifications the activity wheels are of the usual type (e.g. Slonaker, 1908; Richter, 1922). In place of the cyclometer usually employed to register the number of revolutions the device illustrated in Fig. 2

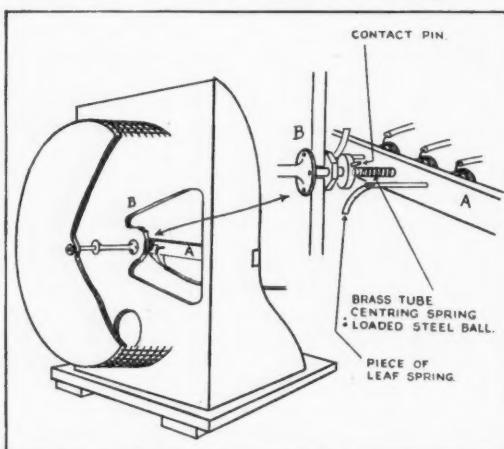


Fig. 2. Construction of activity wheel. For lettering see text.

was used. This consists of a contact-pin attached to the axle of the wheel which, as the wheel rotates, presses against two pieces of watch spring soldered to the shafts of two terminals. A third terminal makes contact with the axle by means of a spring loaded ball-bearing riding in a recess at the end of the axle. Leads are taken from these terminals to the recording unit so that, as the wheel revolves, two independent circuits are alternately made and broken. These two circuits are thus similar to those already described for the activity galleries.

The resting accommodation for the rat is made very small so that all locomotor activity must take place in the wheel. Food and water are available from a food basket and drinking bottle attached to the living cage.

Experimental Procedure

Eight adult female rats were used in natural lighting, four being placed in activity galleries and the other four in activity wheels. After 48 days the rats in the wheels were placed in the galleries, and vice versa, for a further 30 days. Food and water were provided ad. lib.

The total distance run each 24 hours and the diurnal distribution of this activity was recorded, the behaviour of each rat in a revolving wheel being compared with its own performance when housed in an activity gallery

Results

All rats were considerably more active when living in the activity wheels than when in the galleries. The mean distance run each 24 hours in the wheels was 6820 ± 1646 yards (standard error of mean of 8 rat averages) while the same animals when housed in the galleries ran only 165 ± 17 yards (8). The size of the standard errors relative to the mean distance run in each situation shows that there was greater variability in individual performances when the rats were running in the wheels.

The level of activity characteristic of individual rats while living in the galleries was poorly correlated with their performance in the wheels. The coefficient of correlation between the two levels of activity, calculated from the mean daily distances run by each rat ($r = 0.182$ for 7 degrees of freedom; $P > 0.05$), shows that

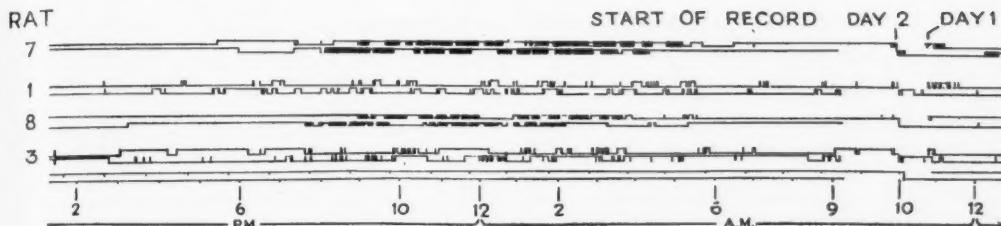


Fig. 3. Comparison of patterns of activity in galleries and wheels. The record shows the temporal distribution of four female rats for two days. Rats 7 and 8 were housed in wheels; rats 1 and 3 in galleries. The times entered on the time scale refer to the second day's activity in each case.

only chance dictated whether an active rat in a gallery would prove to be an active one in a wheel or vice-versa. In fact, the most inactive rat in a gallery was among the most active in the wheels and by far the poorest runner in a wheel was by no means the most sluggish in a gallery.

Activity taking place in wheels was concentrated remarkably consistently into the hours of darkness between 7 p.m. and 4 a.m., very little occurring outside these times. On the other hand, activity in the galleries, while being greatest during the same period was more sporadic and extended over a longer range. Fig. 3 gives a typical example of the records from which these observations were made.

A further difference in the behaviour of rats in the two types of apparatus was that the distance run daily in activity wheels started at a low level and, after an interval varying in length from rat to rat, progressively increased until it fluctuated about a steady mean. The activity of rats placed in the galleries showed no such increment and, if the record for the first day (much of which is frequently devoted to exploratory activity) be discounted, the rat settles down immediately to its characteristic daily performance. These observations are illustrated in Fig. 4 which shows the change in behaviour of two rats, the first after being transferred from a gallery to a wheel and the second from a wheel to a gallery. The figure also shows that the fluctuations of activity which accompany

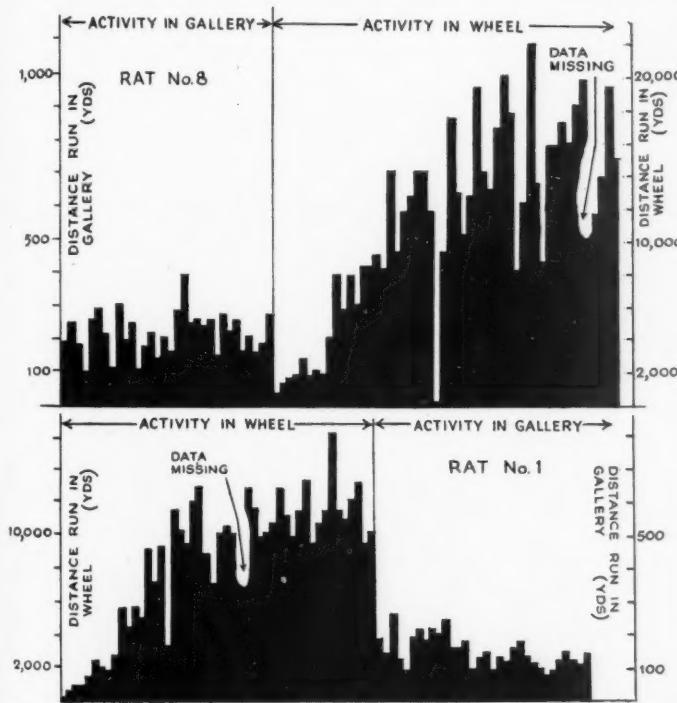


Fig. 4. Change in pattern of activity on transferring female rats from galleries to wheels and vice versa. The time scale is in days, and the scale representing the distance run each day in the galleries is 20 times greater than that for the wheels.

the oestrous cycle in the female are less marked when the rats are kept in galleries than when in wheels. The oestrous cycle of activity is masked during the period of increment which ensues after the rat is placed in the wheel, but reappears once a steady level of activity has been reached.

Yet another difference of behaviour associated with the two types of apparatus was reflected in the mode of deposit of the faeces. The faeces of rats housed in galleries were dropped almost entirely in an arc of approximately 120° centred about the food box. During the first days after being placed in the wheels, rats dropped their faeces in the living compartment (which also housed the food basket) and none beneath the wheel. Later, however, as activity in the wheel increased, more and more faeces were dropped beneath the wheel until, with a fully habituated rat, it was rare to find any faeces at all under the living cage. The position of the faeces under the wheel suggested that all rats faced the same way when running, the direction of running being invariably away from the source of light and towards the wall.

Discussion

The performance of rats in activity wheels of the type used in this experiment is well known. Rats do not immediately run at their characteristic levels of activity when placed in this apparatus and the period during which daily increments in activity take place may be regarded partly as one in which the animal becomes habituated to an unfamiliar environment and partly as one in which it learns to use the wheel for its exercise. In the light of the present results, the period of 10 days suggested by Shirley (1928) for these processes would seem to be inadequate, for most rats usually took about three weeks to reach their normal level of activity. Billingslea (1940) has shown, however, that this period is related to the readiness with which the rats become emotionally adjusted, "emotional" rats requiring longer for habituation but eventually running greater distances than "unemotional" animals. The present results are in agreement with this observation for there was good correlation between the length of time taken by individual rats for habituation and the mean distance covered daily after habituation. The fact that rats placed in the galleries are almost immediately habituated to their new environment may be

attributed to the structural similarity between the galleries and the cages in which they have lived from birth.

It is now clear that the female rat reacts quite differently to the two environments, although the activity taking place in both might be expected to be "spontaneous." These differences in behaviour must be related to some property of the apparatus used, for during the experiment all other sources of stimulus were standardised. The reason why activity in the wheels should so greatly exceed that in the galleries is, however, far from clear. Tinbergen (1950) regards much apparently random activity as "appetitive behaviour" by means of which the animal seeks, or encounters by chance, a stimulus adequate to release some more specific behavioural response. The increased activity of the female during the oestrus is probably of this type. If the relatively small amount of activity in the galleries be regarded as the level of appetitive behaviour of a rat confined in a restricted space, then it is apparent that the considerably greater activity in the wheels is unlikely to consist of appetitive behaviour alone. In this light, activity in the wheels may be divided into two components: appetitive behaviour which is present also in the galleries, and a superimposed element which is released by some stimulus present in the wheel. Alternatively this additional activity may represent a displacement reaction resulting from the frustration of the development of a pattern of behaviour which can be completed in the galleries but not in the wheels.

Other differences in the behaviour of rats used in the two types of apparatus seem to be related to their feeding habits. Rats eat at regular 2-3 hour intervals throughout the day (Richter, 1927), and since visits to food and water would be recorded in the galleries but not in the wheels this could partly account for differences between the two types of apparatus in the diurnal distribution of activity. At the same time, the amount of activity taking place in the galleries during the daytime exceeded that necessary for eating and drinking alone. Richter (1927), using stabilimeter cages, showed that visits to food and water were preceded by activity, but did not distinguish in his findings between running and such non-locomotor activities as vigorous cleaning, scratching and shifts of bodily position within a small space

which would not be recorded in the galleries. The present data for the galleries suggests that running may form part of the restless behaviour described by Richter, but does not show whether it takes place before or after feeding. It is clear, however, that as far as the wheels are concerned, no running associated with feeding takes place during the daytime, and the fact that faeces were dropped exclusively under the wheels and not under the living compartments suggests that any such running taking place during the night must occur after eating and not before.

It seems therefore either that the pre-feeding activity described by Richter does not include a running component, or that if it does the releasing stimulus for this activity is not present in the activity wheel. On the other hand, the wheel provides a situation, absent in the stabilimeter cage, which favours the perseveration of running. The nervous mechanisms which underlie these differences are undetermined, but it is apparent that the stabilimeter cage and revolving wheel measure quite different aspects of spontaneous activity and that results obtained by use of the two techniques cannot unreservedly be interchanged.

Summary

1. The diurnal activity of adult female rats living in stabilimeter cages has been compared with their performance when housed in activity wheels.
2. The results show that in each 24 hours the female rat runs considerably less distance in a stabilimeter cage than in an activity wheel. Furthermore the rhythmic activity normally associated both with daylight and darkness and with the oestrous cycle is less marked when animals are living in stabilimeter cages than when they are housed in activity wheels.
3. Variation between animals in the distance run daily were more marked when the animals were running in wheels than when in stabilimeter cages. There was no significant correlation between the levels of activity of individual rats in wheels and stabilimeter cages.
4. When living in activity wheels the rats were at first relatively inactive and did not reach their characteristic activity level for about 21 days. In stabilimeter cages, the same rats settled down immediately to a steady daily performance.

5. These differences show clearly that the two techniques measure components of activity which have different motivational significance. Activity in a wheel satisfies a need which is not present when the animal is housed in a stabilimeter cage. The possible nature of this need is discussed.

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The Suppression of Audiogenic Hyperexcitement by Learning in *Peromyscus maniculatus*

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Introduction

The sequence of acts constituting audiogenic hyperexcitement in *Peromyscus* has been described by Chance & Yaxley (1949). This paper should be consulted for details of the different phases of the sequence, but briefly, whenever a confined *peromyscus* is subjected to the sound of a whistle, jingling tubes or the sound of an air blast, it alternatively crouches and makes wild dashes around the container, finally losing its balance in a clonic or tonic convulsion.

The possibility that this behaviour could be suppressed by learning was suggested by a single instance when an animal which had escaped from the experimental set-up subsequently gave no response to the auditory stimulus.

Design of Experiments and Methods

In the course of five years of experiments involving repeated daily or twice daily stimulation (jingling of tubes), we have confirmed the observations of Watson (1939) who has shown that the animals of this strain are susceptible to audiogenic hyper-excitement during pre-adult life for a period varying from a few weeks to as long as seven weeks. During this time the sensitivity of each animal is constant for periods of time, and members of a litter appear to show less variation between themselves than animals taken from different litters. The periods vary in length, but the change in pattern of response as the animal grows older, is the same for most animals.

Of 22 animals subjected to prolonged testing twice daily, one died on the 18th and one on the 22nd test; one completed a series of 18; two of 29; two of 31; four of 40; and 11 of 41. When the tests were stopped, one animal ceased clonus behaviour after the 18th test and gave no further reaction to the tubes on repeated

subsequent stimulation. The tests on all the animals were started when they were between three and four and a half weeks old.

At one extreme a few animals reach the terminal phase after a few occasions only; usually these animals show tonus behaviour, but they may start with a few clonic movements after which this behaviour suddenly ceases between one occasion and another. At the other end of the variation were animals which showed an initial period of bouncing, followed by a long period during which clonus regularly occurred, finally passing into a period when tonus was the rule. During the transition from one to the other, an occasional reversion to the type of the previous phase was seen. Finally the animal becomes insensitive to the action of the tubes abruptly from one test to another. The terminal* behaviour ceases only at the end of the phase when tonus is repeatedly present, and this phase itself is frequently met with in animals between six and ten weeks old. When the terminal phase fails to develop, very few signs of hyperexcitement remain. Between the two extremes patterns an intermediate type was sometimes observed in which the responses were less consistent, and the animals on occasion did not respond to the jingling of the tubes, though usually these animals showed some form of excited behaviour.

These observations made it essential to carry out repeated consecutive tests on an animal before and after a procedure designed to alter the nature of subsequent responses to the tubes; only by this method is it possible to show which type of animal one is dealing with, and whether the responses to the tubes are sufficiently consistent for the subsequent observations to reveal a change in the behaviour. This consideration

* "Terminal is here used in place of the word "convulsive" in the previous publication by Chance & Yaxley (1949).

underlies the plan of the observations reported here.

The animal was placed in a smooth-surfaced container (in this instance a sink measuring 32" long \times 14" wide \times 7" high), under a constant illumination from a 60 watt bulb 2' feet above the floor of the container. The tubes (Chance & Yaxley, 1949) were suspended above the centre of the container at the same distance. During all observations up to date, the tubes have been rung at a constant speed for three minutes, or longer. The speed of the tube jingling was maintained constant by an electrically driven shaker controlled through a rheostat. This type of stimulation produced an induction phase of 20-30 seconds, and a period of pre-consummatory hyperactivity lasting approximately from 30-60 seconds in most instances, extending up to two minutes in a few cases. The terminal phase lasted only 10-15 seconds, and was followed by periods of salta-

tion or catalepsy or less often merely by exhaustion. Saltation usually lasted between 20 and 30 seconds, though it has sometimes lasted up to three minutes; catalepsy may last two or three minutes, analgesia was present up to 60 minutes following recovery of the animal. The tubes were stopped as soon as the animal entered the terminal stage.

In the experiments reported here, each animal was tested on successive days or twice daily on successive days for a period sufficiently long to show what type of response the animal gave to the tubes. A hut made of plasticene (4" \times 1 $\frac{1}{2}$ " \times 1 $\frac{1}{2}$ ") was then introduced on one occasion, and the animal allowed to explore the container with the hut in it for two minutes or longer if stated, prior to starting the tubes. Usually the mouse found the hut and entered, and sometimes came outside the hut before the tubes started. If the mouse did not enter, a small amount of guidance from the experi-

TABLE 1. (TEST 1)

ANIMAL MARKS		DAILY STIMULUS AT 10 a.m.												DAYS AFTER INTRODUCTION OF HUT											
		DAYS BEFORE INTRODUCTION OF HUT												DAYS AFTER INTRODUCTION OF HUT											
LITTER 1	FR	6	5	4	3	2	1	H	1	2	3	4	5	6	7	8	9	10	11	12					
	P	T	T	T	T	T	T	-	-	-	B	B	T												
	FL	T	T	T	T	T	T	-	-	-	B	B	T												
	IL	T	T	T	T	T	T	-	-	-	B	T	T												
	L	T	T	T	T	T	T	-	-	-	T	T	T												
LITTER 2 (FEMALE)		T	T	T	T	T	T	-	-	-	T	T	T												
		T	T	T	T	T	T	-	-	-	T	T	T												
LITTER 3 (MALE)		T	T	T	T	T	T	-	-	-	-	-	-										B	T	T
																						D	X	X	X

Explanation of Capital Letters used instead of Signs.

- T — Tonic Terminal Behaviour
- B — Bouncing Terminal Behaviour
- C — Clonic Terminal Behaviour
- X — Different Operator
- H — Hut present
- S — Horse-shoe present
- D — Different Container used

- K — Tubes were rung in room with animals in keeping cages
- m — Experiment at 10 a.m.
- e — Experiment at 4 p.m.
- P — Photographs taken
- — No hyperexcited behaviour
- U — Unspecified type of terminal behaviour

mentor's hands brought it to the entrance of the hut and it would then invariably enter. If it did not come out before the tubes were started, then the hut was gently removed and the mouse pushed to one side, the hut being restored to its original position, so that in every instance the tubes were started with the animal outside the hut. These manipulations were necessary only occasionally.

Throughout these experiments the mice were kept together in litters in small mouse boxes of dimension 10" x 6" x 4" littered down with sawdust and plenty of wood-wool. The test was carried out after these boxes had been removed from the test room, and the particular animal under observation had been transferred to the container in the test room.

RESULTS

Test 1 (Table I) was made with six animals, each subjected to the sound of the tubes consecutively on six occasions, and a plasticine hut was introduced on the seventh day to provide a means of escape by taking refuge in it. On all these occasions the tubes were rung for

three minutes and the hut, while present from the start, was removed half a minute, after the sound was begun. On the seventh day none of the animals reacted, and this was true on the eighth and ninth day. It had been intended to carry on the observations in the absence of the hut after the occasion when it was present for six consecutive days as this would have provided sufficient material for statistical treatment had the animals reacted in a variable manner. However, it was necessary to change the observer on the third day, after the introduction of the hut, and this had the effect of restoring the hyper-excited behaviour in these animals. The animals in litter three, which had been started five days earlier and had been run on with the other five, also reacted again in the presence of the new observer. These observations despite the unexpected effect of a different operator, showed that the phenomenon observed on the occasion when the animal jumped out could be repeated with a hut as a form of refuge.

The second test (Tables II and III) involved nine animals from two litters. They were subjected to twice-daily tests for seven days,

TABLE II. (TEST 2)

	1 m e	2 m e	3 m e	4 m e	5 m e	6 m e	7 m e	8 m e	9 m e	10 m e	11 m e	12 m e	13 m e	14 m e	15 m e	16 m e
Litter 4 P	---	-		UU	-U	UU	UU	---	---	-		C	C	C	C	C
												H				
FR	-	-		UU	UU	UU	UU	-	---	-		C	C	C	C	C
												H				
IL	UU	UU	UU	UU	UU	UU	U-	UU	T	-	-	C	C	C	C	C
									H							
IR IL	-	-		UU	-U	UU	UU	---	---	-		C	C	C	C	C
												H				
FL	UU	TT	-	-	C	C	C	C	C							
									H							
IR	UU	UU	UU	UU	UU	-U	UU	UU	---	-	-	C	C	C	C	C
									H							
Litter M P	UU	UU	UU	UU	UU	-U	UU	UU	-T	TT	T	T	T	T	T	T
									H							
IR	UU	TT	TT	T	T	T	T	-TT	TT							
									H							
IL	UU	TT	TT	T	T	T	T	T	TT							
									P	P	H					

TABLE III (TEST 2)

	17 m	18 m	19 m	20 m	21 m	22 m	23 m	24 m	25 m	26 m	27 m	28 m	29 m	30 m	31 m			
Litter 4																		
P	C	-	-	-	T	T	T	T	T	T	-	-	-	T	T	T	T	T
	H										S			K				
FR	C	-	-	-	T	T	T	T	T	T	T	-	-	-	T	T	T	T
	H										S			K				
IL	C	-	-	-	T	T	T	T	T	T	T	T	T	T	T	T	T	T
	H										S			K				
IR IL	C	-	-	-	T	T	T	T	T	T	T	-	-	-	T	T	T	T
	H										S			K				
FL	C	-	-	-	T	T	T	T	T	T	T	T	T	T	T	T	T	T
	H										S			K				
IR	C	-	-	-	T	T	T	T	T	T	T	-	-	-	=	T	T	T
	H										S			K				
Litter 5																		
P	T	-	-	-	T	T	T	T	T	T	T	-	-	-	T	T	T	T
	H										S			K				
IR	T	-	-	-	T	T	T	T	T	T	T	T	T	T	=	T	T	T
	H										S			K				
IL	T	-	-	-	T	T	T	T	T	T	T	T	T	T	T	T	T	T
	H										S			K				

(fourteen occasions in all). Three animals reacted continuously throughout the period, three failed to react on a single, though different, occasion, and the other three reacted more or less consistently after an interval had been allowed from the evening of the second day to the morning of the fourth. From the chart it will be seen, therefore, that apart from a few random occasions, these animals reacted consistently for at least eight occasions before the morning of the eighth day on which the hut was introduced for the first time. This had the effect of immediately suppressing hyperexcitement on that occasion, and on four subsequent occasions in four of the animals; two failed to react on the day when the hut was introduced, but gave negative reactions on the four subsequent occasions; another reacted similarly, but was positive on the day of the hut and the day following. Two showed no change in their behaviour. Following this an

interval was allowed from the morning of the 10th day to the evening of the 11th day, and this restored the hyperexcited behaviour to all the animals. Repeated twice-daily tests were then continued until the morning of the 17th day with the same result as previously, (i.e. the evening of the 17th day when the hut was with only occasional negative reactions). On re-introduced, all the animals failed to develop hyperexcited behaviour, and maintained this reaction for three subsequent occasions, after which a similar interval restored hyperexcitement to all the animals.

At this point it was thought important to test whether the sheltering properties of the hut resided in the fact that the hut enabled the animals to get away from the sound, or whether it was the form of the refuge, and so a horseshoe of the same dimensions was introduced in the evening of the 24th day after eight consecutive hyperexcited responses had been elicited

in all the animals. The horse-shoe suppressed hyperexcited behaviour in five out of the nine animals, and this suppression was maintained in the absence of the shoe on three subsequent days. The four remaining animals reacted with hyperexcitement throughout. An interval was then allowed, but owing to a mistake, the tubes were rung in the room when the animals were in their keeping cages, and so a further interval was allowed after it had been found that some of the animals were still showing negative responses; especially since one of the animals which had not been affected by the shoe, was found to give a negative reaction on the evening of the 17th day. In the remainder of this test the behaviour of the animals became irregular, and since all the animals became negative on the morning of the 35th day, if not before, and remained so until the evening of the 45th day, it must be assumed that these animals had reached the end of the adolescent period in which hyperexcited behaviour can be elicited in them.

In addition, 11 animals from two litters were tested with variable and inconclusive results. Fifteen out of 26 animals tested showed the response; nine on more than one occasion.

DISCUSSION

Many workers on "audiogenic seizures" emphasise the great variability in response to the stimulus not only between animals, but also of the same animal at different times. The present observations bear directly on this variability and demonstrate a new and important contributory factor, namely the possibility of a learnt refractoriness to the stimulus modifying the subsequent behaviour of an animal after it has once shown a negative response.

The "shelter" reaction demonstrated by Griffiths (1942) has been independently discovered in this laboratory. The experiments, though conducted in some minor respects differently from those of Griffiths, (i.e. Griffiths provided shelter through a trap door, whereas in this work a shelter in the form of a hut was present from the start and then removed), took account of the fact that the behaviour at

the start of hyperexcitement differs from that which follows later. In his monograph Griffiths (1942) refers to an "oriented" phase preceding the later stages in which the seizure itself takes place. The same distinction was made in an earlier publication (Chance & Yaxley, 1949) in which a controlled period of activity was recorded preceding a later un-controlled phase. In both the experiments of Griffiths and the present studies the shelter was provided in the earlier controlled phase when orientation of movement was present. This makes the results comparable in essential detail, the only difference lies in the fact that additional information has been provided by the present experiments through repeated observations of the response to auditory stimulation on several occasions following that on which the shelter was present.

Recently Marx & Van Spancheren (1952) using a method involving a response, which the rat finds difficult to learn, produced statistical evidence that suppression of the seizures is possible by learning, but it is not possible to discuss the relative success of the two types of test without reassessing the current concepts of the nature of audiogenic hyperexcitement.

Summary

- (1) Evidence is presented which shows that, provided a shelter is present on one occasion when the sound is on, the animal can learn to suppress the hyperexcited behaviour when on subsequent occasions it is submitted to the sound in the absence of a shelter.
- (2) The maintenance of the learnt response is dependent on the repetition of the tests (without the shelter) at intervals less than 30 hours.

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Dorsal Light Reaction of Flying Insects

In their interesting paper on locust behaviour (this Journal, October, 1953), R. C. Rainey and C. Ashall suggest that locusts flying in a light beam may react similarly to swimming animals exhibiting dorsal light reactions.

In this context readers might be interested in a paper by H. Mittelstaedt (Physiologie des Gleichgewichtssinnes bei Fliegenden Libellen, 1950, *Zs. Vergl. Physiol.* 32, 422-463) in which extensive experiments demonstrating the existence of the dorsal light reactions in a dragon fly, *Aeschna imperator*, can be found. Mittelstaedt describes how these dragon flies, when flying in a dark room, with a large, illuminated globe of translucent glass in the middle always turned their backs towards this source of light. Slow flying animals frequently sideslipped when flying level with the lamp, while those flying on top of the lamp with their back downwards crashed. Hovering was altogether impossible except under the lamp. On the other hand,

rapid side turns and even vertical loops with the lamp as centre were observed. More accurate measurements were performed with the aid of a suspending device which prevented the flying insect from moving and falling, while allowing it to orientate in its sagittal plane. Dragon flies suspended in this way turned their backs as long as they "flew" towards a source of light, regardless as to whether this was held above, below or besides the animal and pointed in general with the dorsal end of their dorso-ventral axis to the "pole of maximum illumination." The physiological mechanisms underlying the dorsal light reflex and its interaction with other means of orientation are as yet obscure but Mittelstaedt has gone a long way to analysing them by numerous intricate experiments.

Anybody interested in the maintenance of flight equilibria in insects will greatly profit from reading this paper.

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Proceedings of the Association for the Study of Animal Behaviour

At an Ordinary Meeting of the Association held at the Zoological Society, Regents' Park, London, on 23rd October, 1953, the following papers were read. The President, Dr. A. Walton, was in the Chair.

CLINICAL OBSERVATIONS ON VARIATIONS IN ORO-FACIAL BEHAVIOUR IN MAN

By C. F. BALLARD

Orthodontic Department, Institute of Dental Surgery, London University

Until recently the aetiology of malocclusion was thought to be a problem of normal and abnormal growth of the jaws. In the last few years, however, careful clinical observation and the results of treatment have demonstrated fairly conclusively that the resting posture of the lips, cheeks, and tongue, and their behaviour during deglutition, speech, and the production of facial expression, are equally, or even more, important factors. This is possible because alveolar bone, which is present to support the teeth and only develops if the teeth are present, responds to very light pressures, as any orthodontist knows. The teeth and their supporting alveolar bone (the dento-alveolar structures), therefore, represent the position of equilibrium between the lips and cheeks externally and the tongue internally. Vertically they are in equilibrium with masticating forces which are much lighter than has been supposed.

It is generally accepted that malocclusions are inherited, but if that is so, and if our suppositions so far are correct, then the inherited characteristics are the posture and behaviour of the oro-facial soft tissues. Clinical observations support this view, and it is the author's contention that comparative studies do also.

In all newborn individuals certain patterns of behaviour have to be mature at birth to react in specific ways to the environment. In the human infant, the neuro-muscular mechanism to maintain the posture of mandible, tongue, lips and cheeks, has to be mature at birth, and so do the behaviour patterns of suckling and breathing.

At least one type of abnormal swallowing behaviour is recognised, and it is a cause of malocclusion. This it has been found almost impossible to change. The supposition is that it was present at birth as a mature pattern of behaviour, probably not the result of intra-uterine environment but probably an innate pattern of behaviour.

Similarly, family characteristics of neuro-muscular behaviour can be found in the production of speech and in facial expression.

The main criticism against the theory that these variations of oro-facial behaviour are innate is that they may be imitative. Evidence is accumulating that this is not a valid criticism. Investigations into the genetics of the neuro-muscular behaviour of the oro-facial muscles are being planned.

THE SEARCHING BEHAVIOUR OF COCCINELLID LARVÆ

By C. J. BANKS

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A study of the manner in which ladybird larvae find their aphid prey on bean plots was started with the object of explaining some of the high mortality of the immature stages of these predators. On bean plots, ladybird egg batches are often laid remote from aphid colonies and the young larvae, after hatching, may not readily find the prey.

The behaviour of larvae newly-emerged from the eggs has an important influence on their survival, for some larvae manage to procure food by attacking unhatched eggs. Such larvae probably have an advantage over their fellows if they can live longer and search a greater area for food. Experiments have shown that larvae fed on one egg of their own species can live,

on the average, almost twice as long as unfed larvae, and the lifetime is extended even more by the provision of 2 or 3 eggs.

The searching behaviour of larvae after their dispersal from the egg shells has been studied on bean leaves, on isolated bean plants and in a clump of bean plants in the laboratory. Larvae appear to search in a random manner and to be unable to perceive the prey until a physical contact has been made, as was concluded by Fleschner (1950). Larvae spend a considerable amount of time searching various parts of the plants already searched and in searching where there are no aphids. The direction taken by a larva is influenced by the chance touching of leaves, with the result that it might wander far away from the prey.

The laboratory studies of the movements of larvae have been extended to the field by using radioactive labels containing radium sulphate attached to late stage larvae, thus permitting their detection at a distance of about 2 feet (see Tomes & Brian, 1946; Brian, 1947). Positions of labelled larvae were recorded at intervals of several days; larvae are able to travel as much as 21 feet in 2 days. In one experiment, a larva whose positions were re-

corded over 8 days, wandered for 4 days before approaching within a few inches of an aphid colony which it apparently did not find. Another larva, placed on a stem heavily infested with aphids attended by ants in a plot of beans, remained on the stem for a few hours only; when it attacked aphids, it was itself attacked by the ants. The larva soon left this plant and discovered another with aphids not attended by ants. Here it remained feeding on the prey for 17 hours after which the experiment was ended.

It is tentatively concluded from these experiments, which are continuing, that ladybird larvae, while capable of making a thorough search of their surroundings, may be inefficient in finding their prey, and it is suggested that this is an important contributory cause of the high mortality suffered by the early-stage larvae.

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IS MODERN ETHOLOGY OBJECTIVE?

By J. S. KENNEDY

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 This paper is reproduced in full on pages 12 to 19 of this issue of *The British Journal of Animal Behaviour*

A STATISTICAL ANALYSIS OF SOME DATA ON INFRA-RED COMMUNICATION IN *Apis mellifera*

By J. B. S. HALDANE and H. SPURWAY

Department of Biometry, University College, London

Von Frisch's data show that the number of waggles made in each straight run of the "waggle dance" follow a simple rule. The first 50 metres of distance are indicated by two waggles, and one more waggle is given for each extra 75 metres. The counts have only been made between 100 and 700 metres, and it is not known whether it holds beyond. The following rule holds for distances between 100 and 3,000 metres. "The number of turns made in 10.5 seconds is 6.6 at 100 metres, and each doubling of the distance subtracts one from this number." Beyond 3,000 metres the rhythm diminishes more slowly. The error of the central bee in a gang

sent out in response to a dance was between 2° and 3°. This is the same as the average error of a human verbal direction such as "NE by E." The standard deviation of directions round this mean was 13-15°. Similar figures were given for distance communication.

These and other figures agree with Spurway's interpretation of the dance as a ritualized intention movement like pointing in dogs, but more complicated. The recipient of the message will only fly out in the direction indicated after following a dancer, and thus automatically performing intention movements for the flight.

Book Reviews

King Solomon's Ring. By KONRAD Z. LORENZ. London: Methuen & Co. (1952). Pp. xix + 202. 15s.

The author is described by Julian Huxley in his preface as one of the outstanding naturalists of our day who has been referred to as the modern Fabre. Although written in popular style for a very wide circle of readers, there is little doubt that the material in *King Solomon's Ring* substantiates this high praise. Lorenz's gifts with living animals are clearly of the highest order, and throughout the whole work there is the stamp of scientific thinking which raises it far above most descriptive works written for lay readers. The subject of animal behaviour will benefit from this text as read by a wider public, and moreover it makes delightful reading even for the professional behaviourist.

Fleas, Flukes and Cuckoos: a Study of Bird Parasites. By ROTHSCHILD, MIRIAM, & CLAY, THERESA. New Naturalist Series Special Volume. London: Collins. 1952. Pp. xiv + 304, 66 illustrations. 21s.

The title of this valuable work is unusual, and so also are its scope and presentation. The documentation, if perhaps less extensive than in more conventional monographs, is nevertheless an adequate introduction for any serious student, and represents a very wide field of study. The text, while concise and to the point as considerations of space necessitate, is essentially readable, and there are charming if unessential drawings to supplement those illustrating the major technical contributions.

Part I (55 pp.) deals with general principles, Part II (102 pp.) with bird fleas and feather lice, and Part III (111 pp.) with protozoa, worms, diptera, mites, "micro-parasites," the fauna of birds' nests, skuas, and the European cuckoo. There follows a carefully compiled biographical appendix. The book will be of value not only to parasitologists and ornithologists, but also to a wide range of zoologists, naturalists and veterinarians. From the standpoint of behaviour, the existence of an absorbing range of problems is clearly indicated, and the fact that the solution of many of them would be of decided economic value does not render them any the less fascinating.

The authors are to be congratulated on their

adequate coverage of a large amount of subject-matter, and the clarity of presentation is itself adequate tribute to the quality of the text. There are some minor errors, but none is serious. One cannot but escape the conclusion that the sex of the authors has in a few instances influenced the choice of subject matter or the emphasis placed upon morphological or behavioural sex-differences in species that are discussed.

The Behaviour and Social Life of Honey Bees.

By C. R. RIBBANDS. London: Bee Research Association. 1953. Pp. 352. 21s.

In this book an eminent explorer of the life of bees surveys our knowledge concerning the biology and the social life of the honey bee and also the historical development of this knowledge. The material is presented in four sections.

I. The Roots of Behaviour. This deals with the performance of the sense organs, which it is necessary to understand for any analyses of the organisation of a bee colony. The role of the highly developed glands of the bees, which in many ways impinge on their social tasks, are also described.

II. Individual Behaviour in the Field. Here the achievement of the individual bees, their orientation in the field, the behaviour during their visits to flowers, their time sense and the nuptial flight are described.

III. Communication between Honey Bees. This section deals with the more recent results concerning communications during foraging and swarming, and with the application of these results in attempting to increase honey and seed production.

IV. Life within the Community. The communal working of a colony is described, e.g., the processing of the food, the production and use of wax, the regulation of temperature and humidity, brood rearing, division of labour, swarming, etc.

Specialist jargon is throughout avoided in the book, which is thus easily understood by laymen. Consequently, the aim of the work, which is to acquaint bee keepers and naturalists with the life of bees, seems well achieved. The details of this communal organisation have since olden times been a subject of marvel for people and new and wonderful faculties of the bees are being again and again discovered.

However, the book is also important for the research worker and scientist, because the literature of all countries is up to date and has been fully and carefully utilized. The author has concentrated on facts and has on the whole tried to avoid speculation; when not enough information is available, a definite point of view is presented, while care is taken to distinguish between observations and the subjective opinions of the author.

The inclusion of as yet unpublished results by the author, who has done considerable work in the field himself, adds to the attractions of the book. Nine very beautiful photographs and many figures in the text should also prove very helpful. The valuable book is sure of a cordial reception by laymen, bee keepers and scientists.

K. v. FRISCH,
Munich.

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Association for the Study of Animal Behaviour

FOUNDED 13TH MARCH, 1936

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OBJECTS.

The Association for the Study of Animal Behaviour is a scientific society, founded in 1936. Its aim is to promote and co-ordinate work in animal behaviour, the study of which is of interest or importance to a wide range of biologists, e.g., those engaged in psychology, physiology, zoology, animal husbandry and veterinary science.

Scientific meetings are held, often in conjunction with other societies, and the Association possesses a library from which members may borrow, and to which all members are asked to contribute copies of their publications. From 1936 to 1952 the Association published at irregular intervals the BULLETIN OF ANIMAL BEHAVIOUR. This has now been replaced by a regular quarterly publication, the BRITISH JOURNAL OF ANIMAL BEHAVIOUR, which contains original scientific papers and reviews.

MEMBERSHIP.

Membership is open to all who have a genuine interest in animal behaviour and whose election is approved by Council and confirmed by a general meeting. The annual subscription is £1 1s. and whenever possible should be paid by Banker's Order. Forms of Application for membership may be obtained from the Honorary Secretary.

THE BRITISH JOURNAL OF ANIMAL BEHAVIOUR

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